Universidade Estadual de Campinas

TAXONOMIA E FILOGENIA DE *DIMEROSTEMMA*, E SUA RELAÇÃO INTERGENÉRICA NA SUBTRIBO ECLIPTINAE (ASTERACEAE: HELIANTHEAE)

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minha mãe

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RESUMO

Dados de seqüências de nove regiões do genoma de cloroplasto foram obtidos para 34 dos 49 gêneros da subtribo Ecliptinae, tribo Heliantheae. As regiões analisadas incluem gene *mat*K; introns *pet*B, *pet*D, *trn*L; e os espaçadores intergenéticos *ndh*I-*ndh*G, *rpl*20-*rps*12, *acc*D-*rbc*L, *trn*T-*trn*L, *trn*L-*trn*F. A árvore de consenso de bootstrap revela que a subtribo Ecliptinae é monofilética, apresentando quatro clados principais. O clado basal corresponde a táxons endêmicos dos Andes e os outros encontram-se agrupados em uma tricotomia com cada um deles fortemente sustentado. Um destes clados contém um agrupamento morfologicamente heterogêneo, no qual se incluem *Dimerostemma*, *Eclipta*, e *Wedelia*. A morfologia comparativa dos táxons é discutida à luz dos resultados das análises filogenéticas e considerações biogeográficas são brevemente apresentadas. Uma segunda filogenia para a maioria dos membros da subtribo Ecliptinae, que é em grande parte neotropical, foi construída para esclarecer as relações inter - e infragenéricas de *Dimerostemma* e *Angelphytum*, utilizando ITS e ETS do DNA nuclear. A árvore de consenso estrito revelou a subtribo Ecliptinae como monofilética com sete clados principais. A maioria dos nós internos apresenta um bom suporte de bootstrap, o que não acontece, no entanto, para os nós basais. O clado composto pelas 18 espécies amostradas de *Dimerostemma* e *Angelphytum* consiste em três subclados principais. Encontra-se fortemente sustentado e é proximamente relacionado com um agrupamento de táxons, em sua maioria norte americanos. A única espécie anual, *Dimerostemma annuum*, apresenta-se basal e grupo irmão dos outros dois subclados. Cada um destes subclados compreende uma combinação de espécies de ambos os gêneros. A espécie tipo, *Angelphytum matogrossense*, encontra-se agrupada com a maioria das espécies de *Dimerostemma* amostradas. Este resultado indicou *Angelphytum* como sinônimo de *Dimerostemma* e as combinações sob *Dimerostemma* foram efetuadas. No Brasil ocorrem dezenove espécies de *Dimerostemma*. A circunscrição de *Dimerostemma* foi elaborada

com o estabelecimento de uma nova espécie, proposição de sinonímias e validação de uma combinação. Todas as novidades taxonômicas aqui propostas serão validamente publicadas em um futuro próximo. O Brasil, com aproximadamente 80% das espécies conhecidas atualmente é o centro de diversidade do gênero. O gênero *Dimerostemma* é circunscrito pelo invólucro com uma série mais externa de brácteas involucrais semelhantes às folhas, pelo papus coroniforme não constrito, constituído por aristas geralmente bem desenvolvidas, robustas e contínuas com as margens da cipsela. É o único gênero da subtribo diferenciado pela presença de fitomelanina na base das aristas. As variações na forma das brácteas involucrais mais externas, ápice das páleas, cipselas do disco e papus revelaram-se caracteres diagnósticos na identificação das espécies. Uma chave, descrições e comentários para os membros brasileiros de *Dimerostemma* foram elaborados. Sinonímias, ilustrações, como também notas sobre distribuição, habitat, fenologia e citação de espécimes foram fornecidas.

ABSTRACT

Sequence data for nine regions of the chloroplast genome have been obtained for 34 of the 49 genera of subtribe Ecliptinae of tribe Heliantheae. The analyzed regions include gene *mat*K; introns *pet*B, *pet*D, *trn*L; and intergenic spacers *ndh*I-*ndh*G, *rpl*20-rps12, *acc*D-*rbc*L, *trn*T-*trn*L, *trn*L-*trn*F. The bootstrap consensus tree reveals a monophyletic subtribe Ecliptinae with four major clades. The basal clade corresponds to taxa endemic to the Andes and the other clade are grouped in a trichotomy with each one strongly supported. One of these clades contains a heterogeneous array of genera including *Dimerostemma*, *Eclipta*, and *Wedelia*. The morphology of these taxa is discussed in the light of the results from the phylogenetic analyses and bio-geographical considerations are briefly addressed. A second phylogeny for a majority of the members of the mostly Neotropical Ecliptinae using the ITS and ETS of the nuclear DNA was constructed to elucidate the inter - and

infrageneric relationships of *Dimerostemma* and *Angelphytum*. The strict consensus tree reveals a monophyletic subtribe Ecliptinae with seven major groups. The majority of the interior nodes has good bootstrap support, but not the basal ones. The clade containing the 18 species of *Dimerostemma* and *Angelphytum* sampled is strongly supported. It is sister to an assemblage of mostly North American Ecliptinae and has three main groups. The only annual species, *Dimerostemma annuum*, is basal and sister to the two other subclades, each containing a combination of species of both genera. The generic type, *Angelphytum matogrossense* is clustered with most species of *Dimerostemma*. This result indicated *Angelphytum* as synonym of *Dimerostemma* and the combinations under *Dimerostemma* were made. Nineteen species of *Dimerostemma* occur in Brazil. One new species, proposal of synonymies and a validation of a combination are proposed for *Dimerostemma*. All taxonomic novelties proposed here will be valid published in a near future somewhere else. Brazil, with approximately 80% of the current known species, is the principal focus of diversity for the genus. *Dimerostemma* is unified by its involucre with an outer series of leaf-like phyllaries, by an unconstricted coroniform pappus with awns mostly well developed, stout, and continuous with the margins of the cypsela. It is the only member of the subtribe differentiated by the extension of phytomelanin from the cypsela body to the base of the awns. The variation in the shape of the outer phyllaries, pales, disc cypsela and papus are all diagnostic in species identification. A key to the Brazilian members of *Dimerostemma*, synonymies, descriptions, commentaries and illustrations are provided, as well as notes on distribution, habitat, phenology and specimen citations.

INTRODUÇÃO

O girassol - *Helianthus annuus* L. - é o membro mais popular da tribo Heliantheae, que inclui também os membros ornamentais, representantes dos gêneros *Cosmos*, *Dahlia* e *Zinnia*. Em sua revisão dos limites tribais e subtribais de Heliantheae, Robinson (1981) destaca que o mais notável ao estudante da tribo é a diversidade refletida nos muitos de seus caracteres óbvios, taxonomicamente úteis, tais como variação na sexualidade das flores, extremos em desenvolvimento de páleas, incluindo formas ornadas ou muito expandidas, e uma grande variação na forma da cipsela e do papus.

A tribo Heliantheae sensu Robinson (1981) inclui Tageteae Cass. e Helenieae Benth. & Hook. f., consistindo de aproximadamente 3000 espécies em ca. de 260 gêneros distribuidos em 35 subtribos. Este autor reconheceu grupos desprovidos de páleas, tradicionalmente referidos à tribo Helenieae s.l. como subtribos de Heliantheae e incorporou alguns táxons previamente incluídos em outras tribos, tais como Senecioneae. Para manter o reconhecimento de uma Heliantheae s.s., supostamente monofilética, Karis & Ryding (1994) restabeleceram a tribo Helenieae s.l. como um grupo parafilético provisório. Na circunscrição destes autores, Heliantheae inclui aproximadamente 2500 espécies em ca. de 189 gêneros (ca. 34 ocorrem no Brasil) distribuídos em 10 subtribos.

Em prol de uma taxonomia para a tribo que melhor reflita suas relações filogenéticas, Heliantheae s.s. foi provisoriamente estabelecida por Baldwin et al. (2002) em essencialmente seu sentido tradicional; Helenieae foi reconhecida no sentido restrito, Madieae e Tageteae foram expandidas, e além disso, três novas tribos foram estabelecidas.

Na mais recente classificação para a família Asteraceae proposta por Panero & Funk (2002), a tribo Heliantheae é uma das 35 tribos da família. A tribo Heliantheae foi recentemente redefinida, contendo somente gêneros com receptáculos paleáceos, brácteas involucrais foliáceas e anteras geralmente escuras (Panero & Funk, 2002;

Panero *et al.* em prep.). Esta nova interpretação das relações filogenéticas em uma tribo Heliantheae mais exclusiva resultou no reconhecimento de somente 10 subtribos. Sua distribuição é predominantemente norte-americana com um grande número de espécies concentradas no México e sudoeste dos Estados Unidos, e comparativamente em menor número nos Andes e sudoeste do Brasil.

Devido à presença de muitos caracteres óbvios que marcam a distinção entre eles, os membros da tribo Heliantheae têm sido tradicionalmente melhor circunscritos que aqueles da maioria das tribos da família Asteraceae (Robinson,1984a). Ressalta-se, contudo, que os membros de Heliantheae da subtribo Ecliptinae, entre os quais *Angelphytum* G. M. Barroso e *Dimerostemma* Cass. se encontram, não têm tido a mesma sorte. Justifica-se desta forma o nosso trabalho, que objetiva esclarecer a posição filogenética de *Angelphytum* e *Dimerostemma* na subtribo Ecliptinae, como também elucidar suas relações filogenéticas e estudar a taxonomia destes dois gêneros.

Os gêneros da subtribo Ecliptinae têm sido geralmente diferenciados por caracteres pouco consistentes, o que leva a relações intergenéricas contraditórias. Desta forma, a subtribo Ecliptinae sensu Stuessy (1977) contém somente 22 gêneros, enquanto a circunscrição de Robinson (1981) para a tribo inclui 66.

Estudos filogenéticos baseados em caracteres morfológicos (Karis & Ryding, 1994) e em sítios de restrição do cpDNA (Panero *et al.*, 1999) revelaram que a subtribo Ecliptinae, como circunscrita por Robinson (1981), não se apresenta monofilética. Estes estudos levaram a uma circunscrição mais exclusiva para a subtribo.

Karis & Ryding (1994) classificaram os gêneros de Heliantheae em 10 subtribos. *Eclipta* L., o gênero tipo da subtribo, ficou entre os 15 gêneros de posição incerta. Assim sendo, a maior parte dos gêneros de Ecliptinae sensu Robinson foram colocados por estes autores na subtribo Verbesinae. Panero *et al.* (1999) reconheceram o clado

contendo *Eclipta* como subtribo Ecliptinae, que em sua maior parte coincide com a circunscrição de "*Wedelia* group" de Karis & Ryding (1994).

Como presentemente circunscrita por Panero *et al.* (1999 e em prep.), a subtribo Ecliptinae consiste de 49 gêneros com a maioria restrita ao México e América Central. Seis destes gêneros, incluindo dois de ampla distribuição, ocorrem no Velho Mundo. Com a exclusão de 5 gêneros ruderais, ocorrem 10 gêneros no Brasil, mas nenhum é endêmico. *Dimerostemma* com 11 espécies (Robinson, 1984a) e *Angelphytum* com 14 (Robinson, 1984b) são singulares na subtribo por apresentarem um número significante de espécies brasileiras.

Angelphytum foi originalmente descrito por Barroso (1980), incluindo uma única espécie, cujos capítulos apresentam todas as flores hermafroditas com corola tubulosa, mas com as cipselas das flores periféricas de forma diversa daqueles das flores do disco. Pelo invólucro com brácteas involucrais externas foliáceas e cipselas aladas, esta autora comparou *Angelphytum* aos gêneros *Zexmenia* La Llave & Lex. e *Dimerostemma* Cass., diferindo do primeiro pela ausência de flores periféricas com corola liguliforme e do segundo por apresentar flores periféricas férteis.

Segundo Robinson (1984b), o caráter "capítulo desprovido de flores periféricas com corola liguliforme", originalmente utilizado para delimitar *Angelphytum*, provou não ser consistente na delimitação genérica, ocorrendo também em espécies de *Zexmenia*, *Wedelia* Jacq. e *Aspilia* Thouars. Assim, o gênero *Angelphytum*, originalmente monotípico, foi expandido por Robinson (1984b) para um total de 14 espécies (três espécies novas e dez combinações, na maioria transferidas de *Zexmenia*).

Sob a redelimitação de Robinson (1984b), *Angelphytum* passou a incluir espécies com flores periféricas férteis, tanto liguliformes como tubulosas. Este autor relacionou *Angelphytum* com *Dimerostemma*, apresentando os seguintes caracteres em comum: hábito herbáceo com xilopódio na maioria das espécies; flores do disco com fauce da

corola cilíndrica; colar da antera distintamente alargado; ramos do estilete das flores do disco contorcidos e geralmente glandulosos; e cipselas do disco geralmente com alas largas.

O gênero *Dimerostemma* apresenta uma história taxonômica semelhante a *Angelphytum*. Originalmente monotípico, também teve sua circunscrição expandida com espécies provenientes principalmente de novas combinações. Quando o gênero *Dimerostemma* foi descrito por Cassini (1817) incluía somente *D. brasilianum*. Cem anos depois, Blake (1917) reconheceu seis espécies para o gênero de Cassini, que incluiam três novas combinações provenientes do conceito amplo de *Oyedaea.* Blake (1917) distinguiu *Dimerostemma* de *Oyedaea* enfatizando as cypselas subquadrangulares e aladas, o papus de aristas robustas e contínuas com as alas, a ausência de escamas entre as aristas e a presença de brácteas involucrais foliáceas.

Robinson (1984a) expandiu o conceito genérico de *Dimerostemma*, incluindo duas espécies novas e transferindo para este gênero mais três espécies brasileiras de *Oyedaea*. Sob a delimitação de Robinson (1984a), *Dimerostemma* passou a consistir de onze espécies distribuídas na Bolívia, Paraguai e principalmente no Brasil.

Também Robinson (1984b), como já observado por Barroso (1980), alertou que o principal caráter distintivo de *Angelphytum*, isto é, a presença de flores periféricas férteis e não neutras, como em *Dimerostemma*, não seria evidência satisfatória para a divisão entre estes gêneros. Por isso, Robinson (1984a) nomeou as brácteas involucrais externas, bem diferenciadas em *Dimerostemma*, que em *Angelphytum* são indiferenciadas ou irregularmente diferenciadas, como mais um caráter distintivo entre estes gêneros.

Com o objetivo de esclarecer as relações inter - e intragenéricas de *Angelphytum* e *Dimerostemma*, levantamos algumas hipóteses. Estes dois gêneros formam cada qual um grupo monofilético? Será que somente juntos formariam um grupo monofilético? Ou será

ainda necessário incluir espécies de outros gêneros para a formação de um grupo monofilético? Estas questões foram abordadas sob o ponto de vista da filogenia molecular a partir de seqüências de regiões do DNA de cloroplasto e do DNA nuclear. Os resultados das análises filogenéticas foram discutidos utilizando-se de morfologia comparativa, procurando refletir os estados de caráter compartilhados entre os táxons dos vários clados.

Conseqüentemente, o primeiro capítulo desta tese refere-se ao esclarecimento das relações filogenéticas de *Dimerostemma* e *Angelphytum* na subtribo Ecliptinae, baseando-se em seqüências de nove regiões do genoma de cloroplasto: gene *mat*K ; introns *pet*B, *pet*D e *trn*L; e os espaçadores intergenéticos *ndh*L-*ndh*G, *acc*D-*rbc*L, *trn*T-*trn*L, *trn*L-*trn*F, e *rpl*20-*rps*12.

O segundo capítulo trata das relações entre as espécies de *Dimerostemma* e *Angelphytum*, contribuindo também para uma maior elucidação das relações entre os demais membros da subtribo Ecliptinae. Com este intuito foram utilizadas as regiões não codificantes do DNA nuclear: ITS ("internal transcribed spacer") and ETS ("external transcribed spacer").

O terceiro e último capítulo desta tese compreende estudos taxonômicos das espécies brasileiras de *Dimerostemma*, incluindo uma chave de identificação, sinonímias, descrições, comentários e ilustrações de uma espécie nova e de caracteres diagnósticos, bem como notas sobre distribuição, habitat, fenologia e citação de espécimes. Visa, assim, facilitar as identificações, providenciar conhecimentos morfológicos para estas espécies e circunscrevê-las taxonomicamente.

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Phylogenetic relationships within subtribe Ecliptinae (Asteraceae: Heliantheae) based on sequence data from chloroplast DNA regions

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Short Running Title: Systematics of subtribe Ecliptinae (Asteraceae: Heliantheae)

ABSTRACT

Sequence data for nine regions of the chloroplast genome, including gene *mat*K; introns *pet*B, *pet*D, *trn*L; and intergenic spacers *ndh*I-*ndh*G, *rpl*20-*rps*12, *acc*D-*rbc*L, *trn*T-*trn*L, *trn*L-*trn*F have been obtained for 34 of the 49 genera of subtribe Ecliptinae of tribe Heliantheae. The genera *Montanoa* and *Rojasianthe* served as outgroups. The bootstrap consensus tree reveals a monophyletic subtribe Ecliptinae with four major groups. The basal clade corresponds to taxa endemic to the Andes including the genera *Idiopappus*, *Kingianthus* and *Monactis*. The rest of the taxa sampled are grouped in a trichotomy with each clade having strong bootstrap support. The morphologically similar genera *Oblivia* and *Otopappus* are sister to each other. The second clade is composed by the genera *Blainvillea*, *Jefea*, *Delilia*, *Synedrella*, *Lasianthaea*, *Damnxanthodium*, and *Calyptocarpus* and the third clade contains a heterogeneous array of genera including *Dimerostemma*, *Eclipta*, and *Wedelia*. The morphology of these genera is discussed in the light of the results from the phylogenetic analyses. Bio-geographical considerations are briefly addressed.

Asteraceae-chloroplast DNA-Ecliptinae-Heliantheae-Neotropics-Systematics

INTRODUCTION

Tribe Heliantheae is one of 35 tribes of the family Asteraceae (Panero & Funk, 2002). The tribe is essentially American in distribution with a few species and genera found in tropical areas of the Old World. The Heliantheae have recently been redefined to contain only genera with paleaceous receptacles with mostly strongly conduplicate pales, foliaceous phyllaries, and mostly black or brown anthers (Panero & Funk 2002, Panero *et al*. in prep.). Other genera with epaleaceous receptacles included in the Heliantheae *s.l.* have been placed elsewhere (Baldwin, Wessa & Panero, 2002; Panero *et al*. in prep.). These results have allowed the reinterpretation of phylogenetic relationships in a more exclusive tribe Heliantheae with the resulting recognition of only 10 subtribes namely, Ambrosiinae, Ecliptinae, Engelmanniinae, Helianthinae, Montanoineae, Pinillosinae, Rudbeckiinae, Verbesininae, Zaluzaniinae and Zinniinae (Baldwin *et al.*, 2002; Panero *et al*., in prep.). This paper focuses on the phylogenetic relationships of subtribe Ecliptinae.

Subtribe Ecliptinae was erected by Lessing (1832) and its concept was later emended by Stuessy (1977) when he merged part of Hoffmann' s (1890) subtribes Verbesininae and Melampodiinae. Subtribe Ecliptinae sensu Stuessy (1977) contained 22 genera representing, as he pointed out, a trend toward smaller and more herbaceous plants with carpellate ray florets and a pappus of 2-3 awns or absent, and essentially very similar on gross morphological features to his own concept of subtribe Verbesininae. Subtribe Ecliptinae was expanded by Robinson (1981) to include most genera of Stuessy's (1977) Ecliptinae, Zinniinae, Verbesininae, and Engelmanniinae. In Robinson's circumscription, Ecliptinae became the largest and morphologically the most diverse subtribe of Heliantheae containing 66 of the approximately 260 genera in the tribe. He justified his new concept of the Ecliptinae as a monophyletic assemblage by stating that most members in the subtribe contained cypselas with striations, distinctive resin duct

patterns associated with fibre sheaths in the disc corolla, and the presence of apparently unique secondary chemical products.

A morphological cladistic analysis performed by Karis (1993), and subsequently adapted as a formal classification in Karis & Ryding (1994), revealed a non-monophyletic subtribe Ecliptinae as circumscribed by Robinson (1981). Karis & Ryding (1994) classified the genera of Heliantheae in 10 subtribes placing the genera *Delilia* Spreng.*, Rensonia* S. F. Blake and *Eclipta* L., included in Robinson's Ecliptinae, among their 15 genera of uncertain position. Because *Eclipta* was not assigned to any of their subtribes, most genera of Robinson's Ecliptinae were placed in subtribe Verbesininae.

To evaluate phylogenetic relationships of subtribe Ecliptinae, Panero, Jansen & Clevinger (1999) analyzed chloroplast DNA (cpDNA) restriction site data for 76 genera of Heliantheae. This work revealed also that Ecliptinae, as circumscribed by Robinson (1981), was non-monophyletic and that members of this subtribe were distributed among four different lineages within Heliantheae. Panero *et al.* (1999) recognized the clade containing the genus *Eclipta* as subtribe Ecliptinae. This result allowed for a narrower circumscription of subtribe Ecliptinae that, for the most part, coincided with the circumscription of the "*Wedelia* group" by Karis & Ryding (1994), based on floral micro-characters and inflorescence morphology. This concept of subtribe Ecliptinae also includes *Clibadium* L. and related genera of the Clibadiinae (sensu Robinson, 1981).

As presently circumscribed, (Panero *et al.*, 1999) subtribe Ecliptinae contains 49 genera with a majority of them restricted to Mexico and Central America and a few others endemic to South America. The genera *Lipochaeta* DC., *Melanthera* Rohr, *Wedelia* Jacq. (including *Aspilia* Thouars) and *Wollastonia* DC. ex Decne. are unusual in the subtribe by being endemic or having a significant number of species native to areas outside the American continent.

We analyse sequence data for nine cpDNA regions in 38 accessions, representing 34 genera of Ecliptinae (as delimited by Panero *et al.*, 1999) and two genera representing the outgroup. The main objective of this study is to clarify the phylogenetic position of the genera *Angelphytum* G. M. Barroso and *Dimerostemma* Cass. and to elucidate their relationship to other members of subtribe Ecliptinae.

MATERIALS AND METHODS

The 38 taxa used in this study, Genbank accession numbers, and their sources are listed in Table 1. The genera *Montanoa* Cerv. and *Rojasianthe* Standley & Steyerm. were used as outgroups based on results from the tribal study of Panero *et al.* (in prep.).

DNA ISOLATION

Total genomic DNA was isolated following the procedures of Doyle & Doyle (1987) using mostly field-collected leaves that were subsequently frozen in liquid nitrogen, or fresh leaves from cultivated plants, either raised from field-collected seeds or transplanted from their original habitat and grown in the greenhouse. In some occasions dried leaves stored in silica were also used.

AMPLIFICATION OF THE cpDNA REGIONS

The cpDNA regions were amplified using the Polymerase Chain Reaction (PCR) in 50 μl reactions. The primers for the amplifications of regions of the chloroplast analyzed in this study, namely: gene *mat*K; introns *pet*B, *pet*D; intergenic spacers *ndh*I-*ndh*G and *acc*D-*rbc*L were designed by Panero & Crozier (2003). Intron *trn*L, intergenic spacers *trn*T-*trn*L and *trn*L-*trn*F were amplified using primers designed by Taberlet *et al.* (1991), whereas the intergenic spacer *rpl*20-*rps*12 was amplified using primers reported by Hamilton (1999).

Amplification of the cpDNA regions was performed under the following conditions: one cycle of 4 minutes denaturation at 95°C, primer annealing at 48°C for 45 sec, primer extension at 72°C for 1 minute, followed by 32 cycles with similar conditions to the initial cycle, except for 1 minute denaturation, and an additional 2 seconds for every successive extension. This was followed by a final extension of 10 minutes at 72°C. PCR products were cleaned and concentrated with ultrafree-MC filters (Millipore Corporation) prior to sequencing. Dye terminator sequencing was done at the University of Texas DNA Sequencing Facility on an ABI 3100 sequencer, following manufacturer's instructions and protocols.

PHYLOGENETIC ANALYSIS

Sequences were assembled into contig files and aligned manually using the program Sequencher 3.1.1 (Genecodes Corporation, Ann Arbor, Michigan, USA). Maximum parsimony analyses were performed using the program PAUP (Swofford, 2001). Analyses were conducted of the entire aligned sequence matrix, with all characters and character-state transformations given equal weight; gaps were treated as missing data. Reliability of clades was evaluated by bootstrap method with heuristic searches for 100 bootstrap replicates (Felsenstein, 1985).

RESULTS

The resulting data matrix contains 8052 characters (base pairs aligned length - bp) including: gene *mat*K and partial sequences for its associated *trn*K introns (2541 bp); introns *pet*B (1148 bp) and *pet*D (1134 bp); intergenic spacers *ndh*G-*ndh*I (553 bp), *rbc*L-*acc*D (536 bp) and *rpl*20-*rps*12 (661 bp). The intergenic spacers *trn*T-*trn*L (272 bp), *trn*L-*trn*F (341 bp) and intron *trn*L (866 bp) correspond to primers a-f as described inTaberlet *et al*. (1991). A region approximately 250 bp from the priming site of primer Tab a (Taberlet

et al. 1991) was excluded from analysis because it was impossible to ascertain the number of base pairs in the poly T and poly A sequences found in this region.

Maximum parsimony analysis of the combined cpDNA data matrix of 34 genera of Ecliptinae and two genera representing the outgroup resulted in 3600 minimum length trees, each with a length of 1105 steps, a consistency index (CI) of 0.63 (excluding autapomorphies) and a retention index (RI) of 0.85. For the aligned cpDNA sequences, 551 of 8052 sites (6.8%) were variable and 299 (3.7%) were phylogenetically informative. The bootstrap consensus tree is shown in Fig. 1.

The bootstrap consensus tree is characterized by a basal clade containing three genera and a major clade including most genera sampled. Support for a monophyletic Ecliptinae is relatively weak with 63% bootstrap value. The first group of Ecliptinae to split includes the genera *Idiopappus* H. Rob. & Panero, *Kingianthus* H. Rob. and *Monactis* H.B.K., all from the Andes of Peru and Ecuador (Fig. 1). The support for this clade is strong with 98% bootstrap value. The major clade contains three main subclades, all having a strong bootstrap support of 100%. The first clade contains the genera *Oblivia* Strother and O*topappus* Benth., a group of straggly shrubs or vines mostly endemic to Mesoamerica (Fig. 1). The second clade contains seven genera with the genera *Blainvillea* Cass., *Jefea* Strother and *Delilia* Spreng. splitting sequentially, leading to a clade containing the genera *Calyptocarpus* Less. as sister to *Damnxanthodium* Strother with a 93% bootstrap support and *Lasianthaea* DC. sister to *Synedrella* Gaertn. with a bootstrap support of 100%.

The third clade contains a heterogeneous combination of genera in a basal trichotomy, which is composed of the genus *Eclipta*, the four species of *Dimerostemma*/*Angelphytum* sampled and a large subclade containing the majority of the Ecliptinae sampled. The monophyly of the *Dimerostemma*/*Angelphytum* clade is strongly

supported with a bootstrap value of 100%. The large subclade is characterized by a polychotomy with five branches: *Wamalchitamia* Strother and *Rensonia* appear as single lineages (Fig. 1); two branches contain two genera each namely, *Perymeniopsis* H. Rob. sister to *Tilesia* G. Meyer (65% bootstrap support), *Trigonopterum* Steetz ex Andersson as sister to *Sphagneticola* O. Hoffm. (94% bootstrap support); and a fifth branch including several genera with bootstrap support of 89%.

This fifth clade is characterized by a basal polychotomy containing the genera *Riencourtia* Cass., *Perymenium* Schrad., *Lundellianthus* H. Rob., *Clibadium* and *Baltimora* L. as single lineages. The rest of the taxa in this clade are distributed in two branches, one containing the genera *Melanthera*, *Wollastonia* and *Lipochaeta* (bootstrap support of 58%) and the other with a strong bootstrap support of 100%, including the genera *Zexmenia* La Llave and *Wedelia* (bootstrap value of 85%) as sister to *Elaphandra* Strother, *Steiractinia* S. F. Blake and *Oyedaea* DC. (each relationship with bootstrap support of 99%).

DISCUSSION

Relationships among the genera of the Ecliptinae have always been controversial mainly because generic circumscriptions are based on tenuous differences in cypsela characteristics. Strother (1991) reassessed relationships among most genera of the Ecliptinae by reviewing carefully cypsela features of most genera in the subtribe and establishing synapomorphies useful in circumscribing groups that appeared to share a common evolutionary history. His studies resulted in the placement of several North American species into new genera. He followed the Ecliptinae concept of Robinson (1981), providing keys for the genera present in North America. Molecular studies by Panero *et al.* (1999) offered a different view of the phylogenetic relationships of the subtribe, establishing that the concept outlined by Robinson (1981) was not monophyletic.

Strother (1991) did not have the benefit of starting his studies on the Ecliptinae with a molecular phylogeny as a guide for character distribution and comparisons nevertheless, his lucid account of the morphology of the group serves as a guide for us to compare and assess the results from our molecular studies.

Recent molecular studies of tribe Heliantheae (Panero *et al.* in prep.) have identified the genus *Montanoa* with 25 species of shrubs and trees (Funk 1982) as basal to the genera of subtribe Ecliptinae and collectively sister to the clade containing *Rojasianthe* (subtribe Rojasianthinae, Panero & Funk 2002) and the rest of the Heliantheae s. str. The same studies support previous findings (Panero *et al.* 1999) concerning the circumscription of subtribe Ecliptinae to include only 49 genera of which 34 are sampled here. The genera not sampled are *Eleutheranthera* Poit., *Exomiocarpon* Lawalrée, *Fenixia* Merrill, *Iogeton* Strother, *Lantanopsis* C. Wright ex Griseb., *Leptocarpha* DC., *Pascalia* Ortega, *Pentalepis* F. Muell., *Plagiolophus* Greenm., *Podanthus* Lag., *Schizoptera* Turcz., *Synedrellopsis* Hieron. & Kuntze, *Tuberculocarpus* Pruski, *Tuxtla* Villaseñor & Strother, and *Zyzyxia* Strother.

TAXONOMIC DISCUSSION

The bootstrap consensus tree (Fig. 1) is characterized by two clades, a basal and a major one containing three main subclades. The discussion will follow clade order from the basalmost to the most derived.

The Monactis clade

This clade is composed of the genera *Monactis*, *Idiopappus* and *Kingianthus*. The resolution of this clade as the basal group of Ecliptinae confirms the results of Panero *et al.* (1999, and in prep.). This clade is comprised by shrubby to arborescent species with alternate phyllotaxy (opposite in the monotypic genus *Idiopappus*). In this group the

cypselas are prismatic, wingless, not constricted below the pappus, and with an annular to shortly cylindrical carpopodium. A possible synapomorphy for the group is to be found in the morphology of the pappus, which consist of a pair of opposite squamellae in *Idiopappus* and a single squamella in various species of *Monactis* and *Kingianthus.*

Although apomixis seems to be comparatively rare in Heliantheae (Robinson *et al.*, 1981), *Monactis* and *Kingianthus* were considered by these authors as the most obvious examples of apomicts in the tribe. Their conclusion was based on the defective anthers of the type specimen of *Monactis dubia* HBK.

The existence of herbarium specimens with flowers showing malformed anthers may be an indication that the population of these species in the collection locality may comprise a combination of hermaphrodite and male-sterile individuals or gynodioecy. Male sterility was observed in species of *Pappobolus* S. F. Blake (Panero, 1992) growing sympatrically with species of *Monactis* and *Kingianthus* in central Ecuador and northern Peru. This breeding system may be more widespread in Andean Asteraceae than previously thought and its documentation anecdotal due to the paucity of herbarium collections or biosystematics studies of the Asteraceae of this region. Therefore, we suggest that gynodioecy should be viewed as a potential alternative explanation to apomyxis in these Andean species.

The biogeography of *Monactis*, *Idiopappus* and *Kingianthus* is also of interest. These taxa is only found along the western slopes of the Andes in central Ecuador and northern Peru, where the general distribution of *Montanoa*, its immediate sister taxon, overlaps with that of *Monactis* and *Kingianthus*. However, the second author has not observed these taxa growing sympatrically. The genus *Podanthus* Lag. was sampled by Panero *et al.* (in prep.) and is sister to this clade. *Podanthus* and the closely related genus *Leptocarpha* DC. are shrubs from the temperate region of Chile and adjacent Argentina and may have reached this area by long distance dispersal or contraction and

expansion of mesic Andean forests by alternating cycles of increased desertification or glaciation events in South America (van der Hammen & Cleef, 1986).

The Oblivia-Otopappus clade

The genus *Oblivia* appears as sister to *Otopappus* in a strongly supported clade. The latter contain 15 species of erect or straggly shrubs found mostly in the tropical deciduous forests of Mexico and Central America (Hartman *Monactis* and *Kingianthus* & Stuessy, 1983). *Oblivia* includes only one species of straggly shrub or vine found in the wet forests of Central America to Bolivia (Strother, 1989). These genera share similar cypselas, which are laterally compressed, narrowly oblanceolate in outline and the pappus awns are not raised on a rostrum. Their cypselas are winged (symmetrically and much more narrowly winged in *Oblivia*, asymmetrically in *Otopappus*) and the wings extend in most especies of *Otopappus* along the entire length of the awns (only to the awn bases in *Oblivia*). The cypsela outline and the insertion of the pappus in the cypsela body in both genera are similar to those seen in most genera belonging to the *Blainvillea* clade. Further sampling may reveal this clade to be sister to the *Blainvillea* clade.

The Blainvillea clade

The composition of this clade is novel as no mention of a close relationship among these genera has ever been proposed in the literature. Most of the annual, ruderal species in the Ecliptinae are included in this clade. Their cypselas are mostly narrowly oblanceolate in outline, attenuate toward the base and the pappus consists of two persistent awns (none in *Damnxanthodium* and *Delilia*). The cypselas apices are obscurely crowned, and the awns, when present, are inserted more or less directly onto the cypsela body. The only genus in this group that shows a distinct rostrum or neck is *Blainvillea*.

As stated by Panero *et al.* (1999) our results also disagree with the placement of *Damnxanthodium* under synonymy in *Lasianthaea*, which was formalized by Turner (1988) and accepted by Karis and Ryding (1994). The monotypic *Damnxanthodium*, endemic to northwestern Mexico, is sister to the ruderal genus *Calyptocarpus*, common from southern Texas south to Central America and the Caribbean (McVaugh & Smith 1967). The alliance between these genera is well supported by bootstrap and is further supported by morphological characters and a similar chromosome number of n = 12. *Damnxanthodium* and *Calyptocarpus* are sprawling to erect perennial herbs branching near the base, with a few heads at the tips and axils of the leafy branches. These genera have a similar narrowly to broadly campanulate involucre, which becomes hemispheric in fruit; the phyllaries are biseriate, herbaceous, subequal and overlapping. They also share similar stramineous to hyaline, membranous pales, which are not keeled (obscurely so in *Damnxanthodium*), a condition rarely seen in Ecliptinae.

The sister relationship of the mainly Mexican *Lasianthaea* and the monotypic *Synedrella*, a widely distributed weed of tropical lowlands, is strongly supported in the present study and supports similar findings by Panero *et al.* (1999). These genera share the same scarious and papery consistency of the inner phyllaries and pales. In addition, the pappus of their disc cypselas is similar, with *Lasianthaea* having projections of small scales or hairs arising from a very short crown between the awns, whereas in *Synedrella*, these projections are reduced to an entire margin.

The phylogenetic relationships of *Delilia* have always been problematical because of the reduced capitulum of only two flowers and its circular phyllaries. In our studies this genus is sister to the clade containing *Lasianthaea* and related genera. *Delilia*, together with *Clibadium*, *Riencourtia* among others with high degree of reduction of its floral parts, were placed by Stuessy (1977) in his subtribe Milleriinae. As explained by Stuessy (1977), this reduction of floral parts were responsible for the difficulties in assessing phylogenetic

relationships of these and the other genera in his Milleriinae. Robinson (1981) rejected the traditional concept of Milleriinae, which was characterized by heads with few flowers, excluding various genera from its circunscription. In this way, Robinson (1981) placed *Delilia* in Ecliptinae and the genera *Riencourtia* and *Clibadium* to Clibadiinae. Our studies show that *Delilia*, *Clibadium* and *Riencourtia* are members of the Ecliptinae and distantly related to *Milleria* L. and relatives now placed in tribe Millerieae (Panero *et al.*, in prep.).

The Wedelia clade

This clade is the largest identified by our analyses and groups a heterogeneous assemblage of taxa. This clade has three main subclades in an unresolved trichotomy namely, *Dimerostemma/ Angelphytum* assemblage, *Eclipta*, and a large one containing most genera of subtribe Ecliptinae endemic to moist forests, exemplified by genera such as *Zexmenia*, *Clibadium* and *Lundellianthus*. Our study is the first to suggest that the pantropical genus *Eclipta* is closely related to and perhaps is the closest extant relative of the mainly Brazilian *Dimerostemma*/*Angelphytum* assemblage.

The characteristically filiform pales of *Eclipta*, its white narrowly ray flowers in several series in *Eclipta prostrata* are unique traits in Ecliptinae. These distinctive characters contributed to its placement among taxa unclassified to subtribe by Karis and Ryding (1994). However, there are some morphological features that are shared between *Eclipta* and *Dimerostemma*/*Angelphytum* group, including cypselas that are narrowed to the base, usually tuberculate and somewhat compressed or 4-angled. In some species of *Dimerostemma* the cypsela wings or pappus or both are very much reduced or lacking. This is exemplified by the cypselas of *D. bishopii* H. Rob., *D. virgosum* H. Rob. and some specimens of *D. annuum* (Hassl.) H. Rob., all resembling the cypsela of *Eclipta*.

Our data support the close relationship of *Angelphytum* and *Dimerostemma*. *Angelphytum* was formally separated from *Dimerostemma* mainly by the fertile ray flower

as opposed to the sterile ray flowers of *Dimerostemma* (Barroso, 1980; Robinson, 1984). The species of this group share a suite of characteristics including: 1) a similar habit, being mostly subshrubs with xylopodium found in the Cerrado biome of savanna-type habitats; 2) outer phyllaries resembling the leaves in form, texture and indumenta; 3) variously winged cypsela not constricted at the apex; and 4) pappus of stout, triquetrous awns that extend from the cypsela body angles. Collectively, these traits also set *Angelphytum*/ *Dimerostemma* apart from the other ecliptinous genera.

The monotypic *Rensonia* and *Wamalchitamia*, a genus of five species, are single lineages in a polychotomy (Fig. 1). In some trees these two genera appear as sisters but in the strict tree their relationship is not supported. These genera share a similar habitat, growing in the forests of southern Mexico and Central America, a similar involucre of subequal phyllaries in 2-series, and overall similarities of the disc cypsela. Despite the minute size of the disc cypsela in *Rensonia* (functionally staminate flowers), both genera share disc cypselas that are trigonous, wingless, narrowly cuneate to linear in outline and their pappus has a hispidulous crown inserted directly on the apex of the cypsela body, not raised on a rostrum.

Perymeniopsis, a monospecific genus endemic to central Mexico, is sister to *Tilesia*, which has a wide-ranging distribution in the Neotropics but is absent from Mexico. The bootstrap support for this relationship, however, is weak (Fig. 1). These genera share a short, mostly biseriate involucre of broad phyllaries, striate pales and truncate cypsela apices. These traits are also shared by *Lipochaeta*, *Melanthera* and *Wollastonia*, although our results show that these taxa do not share a closely common evolutionary history with *Perymeniopsis* or *Tilesia* (see Fig. 1).

In addition, *Perymeniopsis*, *Melanthera*, *Perymenium*, and *Steiractinia* share a pappus that consists of deciduous bristles arranged more or less radially. Robinson (1981) considered the pappus of *Perymeniopsis* as transitional between these genera

given that its squamellae are inserted at a level above the two whorls of bristles. Because of its pappus morphology, straggly habit, and broadly ovate to elliptic shiny leaves, *Perymeniopsis ovalifolia* (A. Gray) H. Rob. has been placed in several genera including *Perymenium* and *Oyedaea*. Our data supports Robinson's view (1978) that *Perymeniopsis* is a distinct genus.

The monospecific genus *Trigonopterum*, a shrub endemic to dry areas of the Galápagos Islands, is sister to *Sphagneticola*, a group of four species of perennial herbs, commonly distributed at lower elevations throughout coastal wet areas of the tropics (Strother 1991). A chloroplast RFLP study by Panero *et al.* (1999) using the same DNA accessions produced a similar result. These authors hypothesized that the evolution of *Trigonopterum* in the Galápagos Islands was the result of a long-distance dispersal event from a tropical American progenitor, probably sister or a species of *Sphagneticola*. In spite of their very different gross morphological features, probably the result of their adaptation to different habitats, the two genera share several floral similarities, such as an urceolate involucre that is hemispheric in fruit, funnelform to campanulate throats of the disc florets, and cypselas that are clavate to pyriform, attenuate or almost stipitate toward the base and strongly tuberculate in maturity. In addition, the two genera have a very similar pappus structure, a well-developed, fimbriate crown.

The largest branch in this clade includes the genera *Riencourtia*, *Perymenium*, *Lundellianthus*, *Clibadium*, *Baltimora*, *Melanthera*, *Wollastonia*, *Lipochaeta*, *Zexmenia*, *Wedelia*, *Elaphandra*, *Steiractinia*, and *Oyedaea* (Fig. 1). Relationships among these genera are not fully resolved. However, the two clades containing eight of these genera were consistently identified by our analyses and that of Panero et al. (1999). The genera *Baltimora*, *Clibadium*, *Lundellianthus*, *Perymenium*, and *Riencourtia* appear as single lineages and relationships among these genera remain unresolved.

The genus *Melanthera* is sister to *Lipochaeta* and *Wollastonia*. Wagner & Robinson (2001) presented an evaluation of the morphology of these genera and concluded that *Wollastonia* and parts of *Lipochaeta* should be included in *Melanthera*. In their study they provided a narrow interpretation of *Lipochaeta* to include only six allopolyploid species, corresponding to *Lipochaeta* sect. *Lipochaeta* (n = 26) as delimited by Gardner (1979). *Melanthera* was broadened to comprise 35 pantropical species, including the species of *Wollastonia* and the taxa of *Lipochaeta* sect. *Aphanopappus* (n = 15) sensu Gardner (1979), containing *Lipochaeta integrifolia* that is sampled here. Our results do not contradict the treatment of Wagner & Robinson (2001) and support taxonomic observations advanced by Gardner (1977), based on chromosome numbers and characters of the involucral bracts and fruits.

A close relationship between these genera is also supported as well by sterile hybrids from crosses made by Rabakonandrianina & Carr (1981) involving *Wollastonia biflora* (as *Wedelia biflora* (L.) DC.) and members of both sections of *Lipochaeta* sensu Gardner (1979). Our results also show that our sample of *Melanthera* (*M*. *nivea*) is only weakly supported (bootstrap value of 58%) as sister to traditional *Lipochaeta* and *Wollastonia* and may suggest that some of the transfers proposed by Wagner & Robinson (2001) may need further assessment. In conclusion, more sampling of these genera is necessary to estimate the validity of the generic realignments proposed by Wagner & Robinson (2001).

The clade containing the genera *Elaphandra*, *Oyedaea*, *Steiractinia*, *Wedelia* and *Zexmenia* was also identified by Panero *et al.* (1999). Members of this clade share a suite of characters including mostly campanulate involucre of 2-3 series of subequal to mostly graduate phyllaries with the outer proximally cartilaginous and distally herbaceous, disc corollas that are narrowly funnelform, cypsela apices that are contracted to a short neck, and pappi of short dentate to fimbriate crowns, with or without awns or bristles. In

addition, the cypselas of this group of plants bear at the base relatively large carpopodia, usually comprised of two distinct shiny plates, and most cypselas in each head bear translucent or opaque elaiosomes between the carpopodial plates (Strother 1991). The only genus in the group in which these structures are minute or not present is *Elaphandra*.

The genus W*edelia* is sister to *Zexmenia* in a branch moderately supported by bootstrap. The species of *Wedelia* of North America were sorted out by Strother (1991) into two groups: one with fertile ray florets and strongly flattened, quadrate or weakly biconvex, usually winged cypselas (traits very similar to those of *Zexmenia*); and the other with neuter rays and nearly pyriform or plumply biconvex, usually wingless cypselas (like *Wedelia tegetis*, sampled here). Despite the differences between these two groups, and between the latter group and *Zexmenia*, the cpDNA results support their affinities. The morphological traits shared by *Zexmenia* and *Wedelia tegetis* are related to the cypsela wings, which when present, are usually extended onto the rostrum and to the pappus, which when present, consist of two to three persistent, rarely fragile, awns.

Zexmenia is currently circumscribed to have only two species (Strother 1991) ranging from southern Mexico to Central America but before Strother's revision, this genus was the repository of all species not conforming to characteristics of other closely related genera. Consequently, several species in this alliance have a combination in *Zexmenia*. Species previously included in *Zexmenia* have been transferred to other genera, including *Lasianthaea* (Becker, 1979), *Jefea* and *Wamalchitamia* (Strother,1991), *Lundellianthus*, and *Angelphytum* Robinson (1978, 1984). Species of *Wedelia* (including *Aspilia*) are distributed mainly in the Neotropics with some species in tropical Africa, summing up to approximately 200 species.

The sister taxa of *Wedelia* and *Zexmenia* are *Elaphandra*, *Oyedaea* and *Steiractinia*. This group of plants are mainly found in northern South America, the cypsela

wings when present do not extend onto the rostrum, and the pappus of awns or bristles when present is fragile and deciduous.

Future studies will concentrate on sampling all members of the subtribe and expanding the chloroplast markers sequenced. Our studies show that as more data is added to the phylogenetic analyses, there is a clear increase in the level of resolution as evidenced by a smaller number of trees and stronger clade support. There is still no consensus as to what approach is better, add more data or increase the number of taxa sampled to obtain solid phylogenetic hypothesis (Graybeal 1998; Hillis *et al.* 2003), however, our experience clearly shows that if the number of taxa is maintained constant, an increase in data points will provide increased resolution. One shortcoming of our study has been the difficulty in obtaining high quality DNA for some taxa of the subtribe as they are widely distributed in the Neotropical region. Herbarium specimens provide enough plant material for a few amplifications but not enough to support larger studies as the one reported herein. Large scale studies aimed at elucidating the phylogeny of tribe Heliantheae and relatives will require extensive fieldwork activities by several individuals working together as the plants are scattered across the Neotropical region and in some instances their collection pose a multitude of challenges.

A molecular approach to elucidate the phylogeny of subtribe Ecliptinae is imperative given the homoplasy in key characteristics shown by many of its members. This homoplasy was visualized by Strother (1991) in his taxonomical studies for the subtribe, and summarized by the following statement: “Affinities or relationships among all the genera of Ecliptinae … often seem to be reticulate. Certain character expressions recur in different combinations among some of the genera”. Our molecular studies show significant homoplasy of key characteristics traditionally used in the classification of Ecliptinae. For example, the cpDNA tree shows that the reduction of the apex of the

cypsela to a short neck or rostrum, a much used characteristic for separating genera within Ecliptinae, appears to have evolved in parallel three times as it is present in genera in different clades including *Blainvillea* in the *Blainvillea* clade; *Trigonopterum* and *Sphagneticola*, sister to each other in the major *Wedelia* clade; and in the group consisting of *Oyedaea*, *Steiractinia*, *Elaphandra*, *Wedelia* and *Zexmenia*, also within *Wedelia* clade.

A character that has also been readily used to delimit groups within Heliantheae is the presence or absence of functionally staminate disc florets in the capitulum. This character appears to have evolved independently at least twice in the Ecliptinae, as it is present in *Baltimora*, *Clibadium*, *Riencourtia* and *Rensonia*, all nested as single lineages within the *Wedelia* clade, and in *Delilia* a member of the *Blainvillea* clade. Our studies have clarified considerably the phylogenetic relationships of the Ecliptinae but more studies, increasing both data and number of taxa, are necessary to have a clear picture of the systematics and evolution of this group.

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Angelphytum bahiense H. Rob.; Brazil: Bahia. *Moraes 447* (UEC); GenBank nos. AY297643, AY297598, AY297609, AY297665, AY297620, AY297632, AY297587, AY297654, AY297676. ***Angelphytum matogrossense*** G. M. Barroso; Brazil: Goias. *Batalha 4027* (UEC); GenBank nos. AY297644, AY297599, AY297610, AY297666, AY297622, AY297633, AY297588, AY297655, AY297677. ***Baltimora recta*** L.; Mexico: Chiapas. *Panero 4487* (TEX); GenBank nos. AY297645, AY297600, AY297611, AY297667, AY297631, AY297634, AY297589, AY297656, AY297678. ***Blainvillea rhomboidea*** Cass.; Brazil: Sao Paulo. *Moraes 657* (UEC); GenBank nos. AY297646, AY297601, AY297612, AY297668, AY297621, AY297635, AY297590, AY297657, AY297679. ***Calyptocarpus vialis*** Less.; Mexico: Nuevo León. *Panero 2342* (TEX); GenBank nos. AY215770, AY214477, AY215394, AY216024, AF383637, AF381338, AY215643, AY215897, AY216149. ***Clibadium alatum*** H. Rob.; Ecuador: Carchi. *Panero 3039* (TEX); GenBank nos. AY215775, AY214482, AY215399, AY216029, AF383642, AF381343, AY215648, AY215902, AY216154. ***Damnxanthodium calvum*** (Greenm.) Strother; Mexico: Durango. *Panero 2252* (TEX); GenBank nos. AY215780, AY214486, AY215403, AY216033, AF383646, AF381347, AY215652, AY215906, AY216158. ***Delilia biflora*** (L.) Kuntze; Mexico: Guerrero. *Panero 2327* (TEX); GenBank nos. AY215781,

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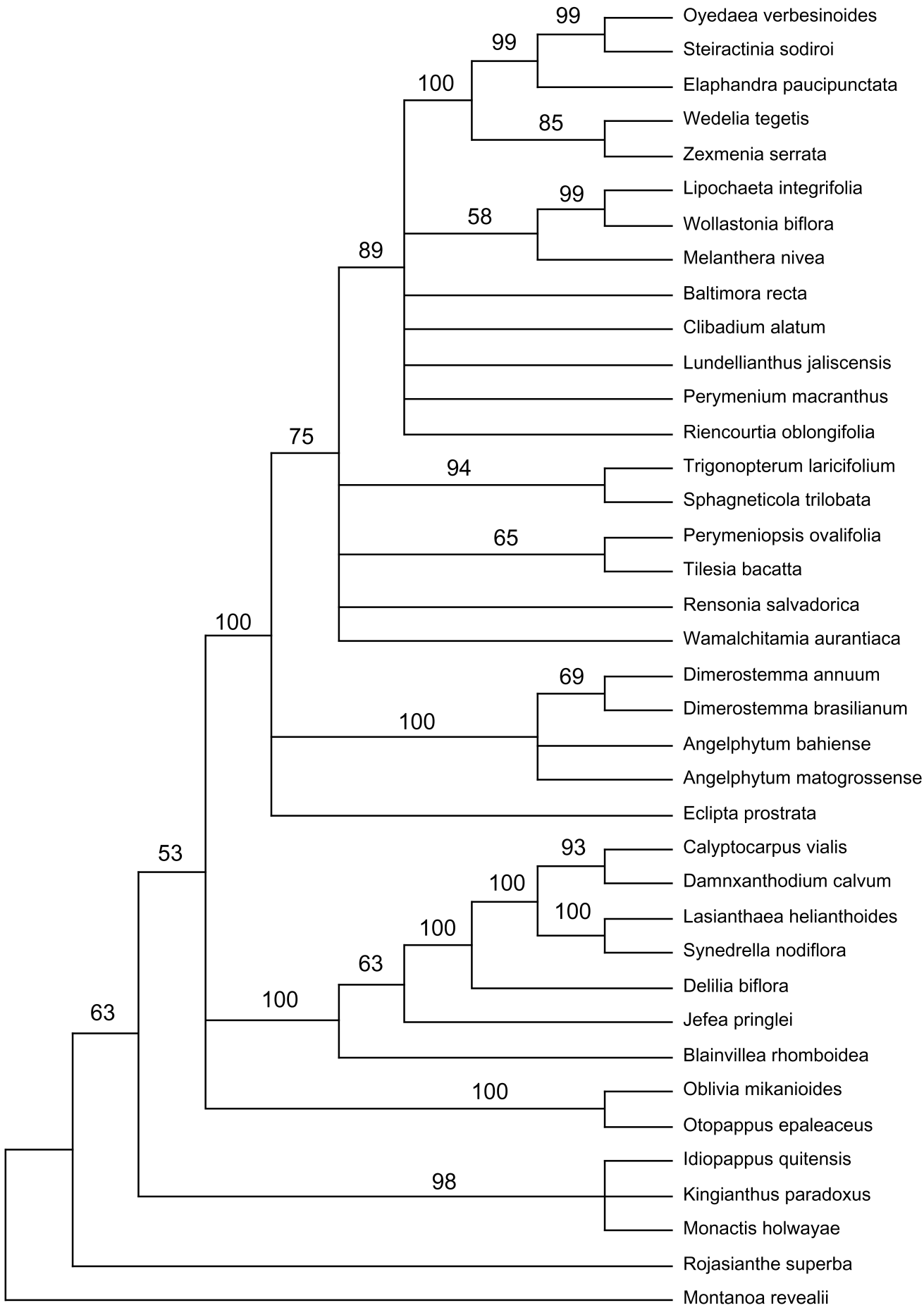
AY216079, AF383693, AF381394, AY215699, AY215953, AY216204. ***Monactis pallatangensis*** (Hieron.) H. Rob.; Ecuador: Chimborazo. *Panero 2907* (TEX); GenBank nos. AY215828, AY214535, AY215451, AY216081, AF383695, AF381396, AY215701, AY215955, AY216206. ***Montanoa revealii*** H. Rob.; Mexico: Oaxaca. *Panero 2480* (TEX); GenBank nos. AY215830, AY214537, AY215453, AY216083, AF383697, AF381398, AY215703, AY215957, AY216208. ***Oblivia mikanioides*** (Britton) J. L. Strother; Venezuela: Aragua. *Panero 2621* (TEX); GenBank nos. AY215832, AY214539, AY215455, AY216085, AF383699, AF381400, AY215705, AY215959, AY216210. ***Otopappus epaleaceus*** Hemsl.; Mexico: Guerrero. *Panero 2515* (TEX); GenBank nos. AY297651, AY297606, AY297617, AY297673, AY297628, AY297640, AY297595, AY297662, AY297684. ***Oyedaea verbesinoides*** DC.; Venezuela: Aragua. *Panero 2609* (TEX); GenBank nos. AY215835, AY214542, AY215458, AY216088, AF383702, AF381403, AY215708, AY215962, AY216213. ***Perymeniopsis ovalifolia*** (A. Gray) H. Rob.; Mexico: Tamaulipas. *Panero 2380* (TEX); GenBank nos. AY215840, AY214547, AY215462, AY216093, AF383707, AF381408, AY215713, AY215967, AY216218. ***Perymenium macrocephalum*** Greenm.; Mexico: Guerrero. *Panero 2274* (TEX); GenBank nos. AY215841, AY214548, AY215463, AY216094, AF383708, AF381409, AY215714, AY215968, AY216219. ***Rensonia salvadorica*** S. F. Blake; Mexico: Chiapas. *Panero 2532* (TEX); GenBank nos. AY215854, AY214560, AY215475, AY216106, AF383719, AF381421, AY215726, AY215980, AY216231. ***Riencourtia oblongifolia*** Gardn.; Brazil: Goias. *Batista da Costa 79* (TENN); GenBank nos. AY215853, AY214559, AY215474, AY216105, AF383718, AF381420, AY215725, AY215979, AY216230. ***Rojasianthe superba*** Standley & Steyermark; Mexico: Chiapas. *Panero 2892* (TEX); GenBank nos. AY215855, AY214561, AY215476, AY216107, AF383720, AF381422, AY215727, AY215981, AY216232. ***Sphagneticola trilobata*** (L.) J. F. Pruski; Venezuela: Portuguesa. *Panero 2639* (TEX); GenBank nos. AY215861, AY213567, AY215482,

AY216113, AF383726, AF381428, AY215733, AY215987, AY216238. ***Steiractinia sodiroi*** (Hieron.) S. F. Blake; Ecuador: Bolívar. *Panero 2993* (TEX); GenBank nos. AY215864, AY214570, AY215485, AY216116, AF383729, AF381431, AY215736, AY215990, AY216241. ***Synedrella nodiflora*** (L.) Gaertn.; Venezuela: Aragua. *Panero 2612* (TEX); GenBank nos. AY215866, AY213572, AY215487, AY216118, AF383731, AF381433, AY215738, AY215992, AY216243. ***Tilesia baccata*** (L.) J. F. Pruski; Venezuela: Aragua. *Panero 2610* (TEX); GenBank nos. AY215871, AY214576, AY215491, AY216122, AF383735, AF381437, AY215743, AY215996, AY216247. ***Trigonopterum laricifolium*** (Hook. f.) W. L. Wagner & H. Rob.; (no voucher, cultivated at Gotheburg University from seeds collected in the Galápagos Islands); GenBank nos. NS, NS, NS, NS, AY297627, NS, NS, NS, NS. ***Wamalchitamia aurantiaca*** (Klatt) Strother; Costa Rica: Guanacaste. *Panero 2719* (TEX); GenBank nos. AY297652, AY297607, AY297618, AY297674, AY297629, AY297641, AY297596, AY297663, AY297685. ***Wedelia tegetis*** Strother; Mexico: Durango. *Panero 2625* (TEX); GenBank nos. AY215879, AY214585, AY215500, AY216131, AF383744, AF381446, AY215752, AY216005, AY216256. ***Wollastonia biflora*** (L.) DC.; USA: Hawaii. (*no voucher, leaves collected by Sterling Keeley in Waimea Falls Park, accession number 75-165*); GenBank nos. AY297653, AY297608, AY297619, AY297675, AY297630, AY297642, AY297597, AY297664, AY297686. ***Zexmenia serrata*** La Llave & Lex.; Mexico: Oaxaca. *Panero 2765* (TEX); GenBank nos. AY215882, AY214588, AY215503, AY216134, AF383747, AF381449, AY215755, AY216008, AY216259.

Figure 1. Bootstrap consensus tree of tribe Ecliptinae and outgroups based on sequence data of cpDNA. Numbers above branches indicate bootstrap values. Bootstrap support is given on the branches for values > 50%. The cladogram has 1105 steps, CI = 0.63 (excluding uninformative characters) and RI = 0.85.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Oyedaea verbesinoides
Steiractinia sodiroi
Elaphandra paucipunctata
Wedelia tegetis
Zexmenia serrata
Lipochaeta integrifolia
Wollastonia biflora
Melanthera nivea
Baltimora recta
Clibadium alatum
Lundellianthus jaliscensis
Perymenium macranthus
Riencourtia oblongifolia
Trigonopterum laricifolium
Sphagneticola trilobata
Perymeniopsis ovalifolia
Tilesia bacatta
Rensonia salvadorica
Wamalchitamia aurantiaca
Dimerostemma annuum
Dimerostemma brasilianum
Angelphytum bahiense
Angelphytum matogrossense
Eclipta prostrata
Calyptocarpus vialis
Damnxanthodium calvum
Lasianthaea helianthoides
Synedrella nodiflora
Delilia biflora
Jefea pringlei
Blainvillea rhomboidea
Oblivia mikanioides
Otopappus epaleaceus
Idiopappus quitensis
Kingianthus paradoxus
Monactis holwayae
Rojasianthe superba
Montanoa revealii

Figure 1

Capítulo 2: a ser submetido à revista Botanical Journal of the Linnean Society

Molecular phylogenetic study of subtribe Ecliptinae with emphasis on *Dimerostemma* (Asteraceae: Heliantheae) based on ITS and ETS sequence data

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Short Running Title: Systematics of Ecliptinae and *Dimerostemma*.

ABSTRACT

A phylogeny for the majority of the members of the mostly Neotropical Ecliptinae (Asteraceae: Heliantheae) using the ITS and ETS of the nuclear ribosomal DNA was constructed to elucidate the inter - and infrageneric relationships of the genera *Dimerostemma* and *Angelphytum*. The genera *Montanoa*, *Rojasianthe* and *Verbesina* were selected as outgroup. The strict consensus tree of nine equally parsimonious trees reveals a monophyletic subtribe Ecliptinae with seven major clades. The basal clade corresponds to taxa endemic to the Andes including the genera *Idiopappus*, *Kingianthus* and *Monactis*. The rest of the taxa are clustered in six main clades, which split sequentially with most deeper nodes collapsing in the 50% majority-rule tree produced by the bootstrap analysis. The clade containing the 18 species of *Dimerostemma* and *Angelphytum* sampled is strongly supported; it is resolved in the strict consensus tree as sister to a an assemblage of mostly North American Ecliptinae, and has three main branches. The only annual species of the genus, *D. annuum* is sister to the two main clades, each containing a combination of species of *Angelphytum* and *Dimerostemma*. The generic type, *Angelphytum matogrossense* is clustered with most species of *Dimerostemma*. This result leads us to consider *Angelphytum* as a synonym of *Dimerostemma* and henceforth all species of *Angelphytum* are formally transfered into *Dimerostemma* (the combinations proposed in this thesis will be valid published in a near future somewhere else). The genus *Dimerostemma* now contains 29 species mostly centered in west central Brazil. The genus is easily separated from other similar composites mainly by its cypselas with a pappus consisting of stout, triquetrous and

tapering awns (sometimes lacking) and a not constricted crown. The new combinations are as follows: **Dimerostemma apense** (Chodat) M. D. Moraes, **Dimerostemma arnottii** (Baker) M. D. Moraes, **Dimerostemma aspilioides** (Griseb.) M. D. Moraes, **Dimerostemma bahiense** (H. Rob.) M. D. Moraes, **Dimerostemma goyazense** (Gardner) M. D. Moraes, **Dimerostemma grisebachii** (Baker) M. D. Moraes, **Dimerostemma hatschbachii** (H. Rob.) M. D. Moraes, **Dimerostemma herzogii** (Hassl.) M. D. Moraes, **Dimerostemma hieronymi** (Hassl.) M. D. Moraes, **Dimerostemma indutum** (Chodat) M. D. Moraes, **Dimerostemma matogrossense** (G. M. Barroso) M. D. Moraes, **Dimerostemma myrtifolium** (Chodat) M. D. Moraes, **Dimerostemma oppositifolium** (A. A. Sáenz) M. D. Moraes, **Dimerostemma paraguariense** (Chodat) M. D. Moraes, **Dimerostemma pseudosilphoides** (Hassl.) M. D. Moraes, **Dimerostemma reitzii** (H. Rob.) M. D. Moraes, **Dimerostemma tenuifolium** (Hassl.) M. D. Moraes,

Angelphytum-Asteraceae-*Dimerostemma*-Ecliptinae-phylogeny-Heliantheae-Neotropics-nuclear ribosomal DNA-Systematics

INTRODUCTION

The genera *Dimerostemma* Cass. and *Angelphytum* G. M. Barroso are endemic to South America with the highest concentration of species found in central-western Brazil. They are classified in tribe Heliantheae subtribe Ecliptinae as emended by Panero, Jansen & Clevinger (1999) as they possess mostly opposite leaves, foliaceous phyllaries, and variously winged cypselas with awned pappus. Collectively the two genera have 29 species and can be distinguished from other members of subtribe Ecliptinae by an involucre with outer series of leaf-like phyllaries, disc corollas with cylindrical upper throats, style branches becoming strongly coiled after anthesis, mostly winged cypselas that are not constricted at the apex and pappus with stout, triquetrous awns of various length or sometimes lacking (Robinson, 1984a; Robinson, 1984b).

The genus *Dimerostemma* was erected by Cassini (1817) to include the species *D. brasilianum* as its only member. A hundred years later, the genus was emended by Blake (1917) to include species from the genus *Oyedaea* DC. that lacked squamellae in their pappus. Robinson (1984a) revised the generic limits of *Oyedaea* by placing in *Dimerostemma* all of its Brazilian species and circumscribing *Oyedaea* to include only species bearing a distinct neck at the apex of the cypsela and mostly restricted to the Andes of northern South America.

Barroso (1980) established *Angelphytum* on the basis of a single species *A. matogrossense*, stressing in its circumscription the eradiate heads and the peripheral, perfect and fertile florets bearing trigonous, 3-winged cypselas. These characters were considered by Barroso (1980) to differentiate her new genus respectively from *Zexmenia*

La Llave & Lex. (with radiate heads) and *Dimerostemma* (with peripheral sterile florets). Robinson (1984b) transferred to *Angelphytum* all the Brazilian species with radiate heads that have been previously placed in *Zexmenia*, justifying in his treatment the unreliability of eradiate heads as a distinguished generic character given that it occurs elsewhere in Ecliptinae as in *Zexmenia* and *Wedelia* Jacq. (including *Aspilia* Thouars).

As the circumscription of *Dimerostemma* and *Angelphytum* became expanded by the transfers from *Oyedaea* and *Zexmenia* and by the discovery of new species of the alliance, the taxonomic concept and limits of these genera grew gradually more obscure. For this reason, the use of ray flower sexuality became increasingly more important and stressed as a convenient character to identify taxa with fertile, pistillate ray flowers placed in *Angelphytum* and those with sterile ray flowers in *Dimerostemma*.

Classification schemes for subtribe Ecliptinae have variously allied *Dimerostemma* to an heterogeneous group of genera. Subtribe Ecliptinae sensu Stuessy (1977) contained only 22 genera and *Dimerostemma* was assigned not to this subtribe but to Verbesininae. In Verbesininae sensu Stuessy (1977), *Dimerostemma* was allied to *Otopappus* Benth. (including its synonym, *Notoptera* Urban) and *Salmea* DC (including its synonym, *Salmeopsis* Benth.) based on mostly opposite leaves, mostly homogamous heads, pappus of long broad awns, short phyllaries and long pales.

The circumscription of Ecliptinae was expanded by Robinson (1981) to contain 66 genera, including most genera of Stuessy's (1977) subtribes Verbesininae, Ecliptinae, Engelmanniinae and Zinniinae. Within Robinson's (1981) concept of Ecliptinae, *Dimerostemma* was associated with *Podachaenium* Benth. and *Oblivia mikanioides* (Britton) Strother on account of being the only members of Heliantheae known to have glands on the abaxial surface of the style branches.

The molecular phylogenetic studies of tribe Heliantheae reported by Panero *et al.* (1999) showed that the Ecliptinae as circumscribed by Robinson is non-monophyletic.

This work supported the removal of *Podachaenium* together with *Verbesina*, *Tetrachyron* and *Squamopappus* from subtribe Ecliptinae to subtribe Verbesininae to contain only these four genera. In addition, the results of Panero *et al.* (1999) placed *Salmea* in a clade outside subtribe Verbesinae or Ecliptinae, but sister to Zinniinae, together with genera, which like *Salmea* have strongly conical receptacles.

As presently delimited, (Panero *et al.*, 1999) subtribe Ecliptinae consists of 49 mostly American genera (34 are sampled here), with the highest concentration of species in Mexico and Central America with some species in South America. This study revealed that the mainly Mexican *Montanoa* is sister group of subtribe Ecliptinae and these two clades are collectively sister of a clade containing *Rojasianthe* (subtribe Rojasianthinae, Panero & Funk, 2002) and the remaining genera of Heliantheae *s. str.*

A phylogenetic analysis of Ecliptinae by Moraes, Panero & Semir (submitted) based on chloroplast DNA (cpDNA) sequences offered support for the view that *Dimerostemma* together with *Angelphytum* comprise a monophyletic group. This was the first study to suggest a close relationship between *Dimerostemma*/*Angelphytum* and the pantropical genus *Eclipta* L. The objectives of the present study were to use sequence data of the internal transcribed spacer (ITS) and the external transcribed spacer (ETS) of the nuclear ribossomal DNA (rDNA) to (1) elucidate the relationship between *Dimerostemma* and *Angelphytum* and (2) clarify their intergeneric relationships within subtribe Ecliptinae.

MATERIALS AND METHODS

SAMPLING

Nuclear DNA variation of ITS and ETS regions were examined for 62 accessions representing 34 genera of subtribe Ecliptinae and three outgroups. A total of 19 accessions were studied for *Dimerostemma* and *Angelphytum*, representing 9 species

each, with two samples for *D. lippioides* (a typical specimen and an intermediate between *D. lippioides* and *D. vestitum*) and including one unpublished new species. The genera *Montanoa* Cerv., *Rojasianthe* Standl. & Steyerm. and *Verbesina* L. were selected as outgroups based on results of Panero *et al.* (1999). The taxa used in this study, Genbank accession numbers, and their sources are listed in Table 1.

DNA ISOLATION

Total DNAs were isolated following the procedures of Doyle & Doyle (1987) from either field-collected leaves subsequently frozen in liquid nitrogen or dried leaves stored in silica. DNA was also isolated from from fresh leaves of cultivated plants (grown in the greenhouse of Universidade Estadual de Campinas) or herbarium specimens. To extract total DNA from herbarium specimens we used the method of Kirsten & Playford (1996).

PCR AMPLIFICATION AND SEQUENCING

The ITS and ETS regions were amplified using Polymerase Chain Reaction (PCR) in 50 μl reactions with 10% DMSO (dimethyl sulfoxide). The ITS region of 18S-26S nuclear rDNA was amplified using primers ITS4 as described by White *et al.* (1990) and ITS5 as modified by Downie & Katz-Downie (1996). In cases where these primers did not provide adequate amplifications, the ITS region was then amplified using the internal primers ITS2 and ITS3 designed by White *et al.* (1990). The ETS region of 18S-26S nuclear rDNA, adjacent to the 5' end of the 18S, was amplified using primers 18S-E and Ast-6 as described by Baldwin & Markos (1998) and Markos & Baldwin (2001). Amplification of the rDNA regions was performed under the following conditions: one cycle of 4 min. denaturation at 95°C, primer annealing at 48°C for 45 s, primer extension at 72°C for 1 min., followed by 32 cycles with similar conditions to initial cycle, except for 1 min. denaturation, and an additional 2 s for every successive extension. This was followed by a

final extension at 72°C for 10 min. PCR products were visualized by agarose gel electrophoresis and purified by filtration, using Ultrafree-MC filters (Millipore Corporation) prior to sequencing. Cycle sequencing of PCR products was conducted with the following settings: initial denaturation at 97°C for 1 min, followed by 30 cycles of 96°C for 30 s, 55°C for 15 s, and 60°C for 4 min. Sequencing products were purified using Centri-seps columns (CS-901, Princeton Separations). The DNA sequences were resolved in an ABI 3100 automated sequencer following manufacturer's instructions and protocols at the University of Texas DNA Sequencing Facility.

PHYLOGENETIC ANALYSIS

Sequences were assembled into contig files and aligned manually using the program Sequencher 3.1.1 (Gencodes Corporation, Ann Arbor, Michigan, USA). Maximum parsimony analyses were performed using the program PAUP (Swofford, 2001). Analyses were conducted of the entire aligned sequence matrix, with all characters and character-state transformation given equal weight, and gaps treated as missing data. Reliability of clades was evaluated by bootstrap method with heuristic searches for 100 bootstrap replicates (Felsenstein, 1985).

RESULTS

PHYLOGENETIC ANALYSIS

Aligned ITS and ETS are 1397 base pair (bp) long (276 bp for ITS1, 166 bp for 5.8S, 255 bp for ITS2, and 700 bp for ETS), 743 characters are constant, 201 are variable but not parsimony-informative and 453 are parsimony-informative (32,4% of the total). Maximum parsimony analysis of the combined ITS and ETS dataset yields 9 equally parsimonious trees with 2088 steps, a consistency index (CI) of 0.423 (excluding uninformative characters) and a retention index (RI) of 0.722.

The strict consensus tree is characterized by the sequential splitting of six major clades (for ease of discussion identified as clades A-F; see Fig. 1) leading to the *Dimerostemma/Angelphytum* clade. Based on ITS and ETS data, *Dimerostemma* including *Angelphytum* species (in boldface, Fig. 1) is a monophyletic genus with 100% bootstrap support. The monophyly of Ecliptinae is weakly supported with a bootstrap value of 53%. Clade A is the basalmost lineage of the subtribe and contains the genera endemic to the Peruvian and Ecuadorian Andes, *Idiopappus* H. Rob. & Panero, *Kingianthus* H. Rob. and *Monactis* H.B.K.

In clade B, *Wamalchitamia* Strother appears as sister group of all the remaining taxa in this clade, but its position is weakly supported (51% bootstrap). The two species of *Lundellianthus* H. Rob sampled form a monophyletic group. *Calyptocarpus* Less. is sister to *Damnxanthodium* Strother (100% bootstrap support); and these genera are collectively sister to *Delilia* Spreng., *Synedrella* Gaertn., *Schizoptera* Turcz. and *Lasianthaea* DC.

The first group to split in clade C is composed by *Sphagneticola* O. Hoffm., which is widely distributed in the coastal wet areas of the tropics, as sister of *Trigonopterum* Steetz ex Andersson, which is endemic to the Galápagos Islands. This relationship has a strong bootstrap support, but not its position in the clade. The position of *Eclipta* in this clade is equally uncertain. *Wedelia simsioides* is not sister to the other two species of *Wedelia* sampled. The two sampled species of *Oyedaea* compose a monophyletic group sister of *Steiractina* S. F. Blake (Fig. 1).

The two sampled species of *Otopappus* form a monophyletic group sister to *Oblivia* Strother and represent clade D (all nodes with 100% bootstrap support). Clade E contains the two species of *Jefea* Strother sampled, which appear as a monophyletic group, but its position in the tree is not supported by bootstrap analysis.

Clade F (bootstrap value of 81) is resolved as sister to the *Angelphytum/ Dimerostemma* clade and is characterized by two main subclades (Fig. 1). One contains

Clibadium L. sister of *Rensonia* S. F. Blake and *Perymeniopsis* H. Rob. Nodes representing these relationships have less than 50% bootstrap support. In the other subclade, *Blainvillea* Cass. appears as sister of a branch containing two groups. The first group includes *Baltimora* L. as sister of *Tilesia* G. Mey, and the second contains *Lipochaeta* DC., *Melanthera* Rohr and *Wollastonia* DC ex Decne as sister taxa of *Perymenium* Schrad.

The *Dimerostemma/Angelphytum* clade is characterized by a basal taxon and two main subclades (Fig. 1). The basal position is occupied by the rare *Dimerostemma annuum*, the only annual species of the group, endemic to Paraguay and neighboring Mato Grosso do Sul, southwestern Brazil. The first subclade (78% of bootstrap) combines most species of *Angelphytum* (in boldface, Fig. 1) together with one *Dimerostemma* species (*D. species nova*).

The other subclade contains the majority of the species of *Dimerostemma.* In this clade, the type of *Angelphytum* (*A. matogrossense*) is resolved in the strict consensus tree as the basal taxon of the branch that includes the type of *Dimerostemma* (*D. brasilianum*). Nested within this subclade, the relatively common and widely distributed *A. arnottii* (west-central and southern Brazil, adjacent Paraguay and eastern Argentina) is sister to the more restricted *A. reitzii* (Paraguay and the adjacent Brazilian states of Mato Grosso do Sul, Paraná and Santa Catarina). The shrubby *D. goyazense*, restricted to calcareous soils in Goiás and neighboring Minas Gerais is sister to this branch. The next branch to split contains *D. grazielae*, from Goiás, sister to *D. episcopale*, from Bahia, both in "cerrado-campo rupestre transition" at the same latitude and altitude. *D. humboldtianum* is basal to the branch containing *D. lippioides*, *D. brasilianum* and *D. vestitum*. This position is supported by 90% bootstrap. *D. humboldtianum* is a relatively rare species, occuring mainly in Brasília, Distrito Federal. *D. vestitum*, *D. brasilianum* and *D. lippioides* are

relatively common in Goiás and Minas Gerais, the two latter species occur sporadically in Mato Grosso and São Paulo.

DISCUSSION

According to the different classification schemes for Ecliptinae various relationships for *Dimerostemma* have been proposed. Likewise, the taxonomic limits of most genera of Ecliptinae have been much disputed because the differences in expressions of key characters among them are usually tenuous. The intergeneric relationships derived from the present phylogenetic analysis help to ellucidate, where data and sampling allow, the taxonomic limits toward the monophyly of the Ecliptinae genera. The discussion of these relationships will follow clade order as they appear resolved in the strict consensus tree from the most basal to most recently derived (Fig. 1).

Clade A. The Andean woody genera *Idiopappus*, *Kingianthus*, and *Monactis* are basal in the subtribe Ecliptinae (Fig. 1). The basal position of these genera in subtribe Ecliptinae is supported as well by similar studies using cpDNA (see Panero *et al.*, 1999 and Moraes *et al.* submitted). The relationship among these three genera is strongly supported as a distinctive group within Ecliptinae. These genera are characterized by their squamiform pappus and mostly alternate leaves. As opposed to most other genera of the Ecliptinae, the species of these genera are large shrubs or trees of the wet forests of the western Andes of Ecuador and Peru. Some species of *Monactis* and *Idiopappus*, along with certain Andean species of *Verbesina*, represent the only arborescent Heliantheae in South America. Arborescent habit within the subtribe Ecliptinae is a plesiomorphic character as it is present not only in species of *Verbesina* but also in *Rojasianthe* and some species of *Montanoa*, all genera used here as outgroup.

Clade B. All genera of this group, except *Lundellianthus*, are characterized by having disc cypselas that are wingless (thin-edged in *Lasianthaea* but not truly winged); in *Synedrella* and *Schizoptera* the cypselas are dimorphic and the ray cypselas have wing like margins. The inclusion of *Wamalchitamia* and *Lundellianthus* in this clade is puzzling, although bootstrap support for these positions are respectively weak (51%) to moderate (85%). Morphology and cpDNA data (Moraes *et al.* submitted) point to a relationship of these two genera with *Wedelia* and *Perymenium* (clades C and F respectively). *Wamalchitamia* is a genus of 4 or 5 species of the lowlands of Mexico and Central America (Strother, 1991), being characterized by having narrowly prismatic cypselas and annular carpopodia. *Lundellianthus* contain 8 species of Central America and Mexico, mostly of Montane Rain forest habitats (Strother, 1989a). It is characterized by mostly winged disc cypselas that are ± quadrate in transection. The monophyly of the two species of *Lundellianthus* sampled is strongly supported. *Lundellianthus jaliscensis* represents the westernmost species of a total of eight in the genus (Strother 1989a), being the only one that occurs beyond the Isthmus of Tehuantepec in Mexico. Because of its broad, scarious phyllaries, *Lundellianthus jaliscensis* at first glance appears to be a member of the genus *Lasianthaea*. Our studies and those of Panero *et al.* (1999) support its inclusion in the genus *Lundellianthus*.

The ruderal genus *Calyptocarpus*, composed by two species that are common from southern Texas to Central America (McVaugh & Smith, 1967) is sister to the monotypic *Damnxanthodium*, endemic to northwestern Mexico (Strother, 1987). This relationship is strongly supported by bootstrap analysis. The present study as well as Panero *et al.* (1999) and Moraes *et al.* (submitted) disagree with the placement of *Damnxanthodium* as a synonym of *Lasianthaea* (Turner, 1988a). *Calyptocarpus* and *Damnxanthodium* share a similar habit, being sprawling to erect perennial herbs that branch near base and have a

few heads at the tips of leafy branches. Their similar stramineous to hyaline pales are not conduplicate or only slightly so in *Damnxanthodium*. The weakly conduplicate pales are rarely seen in the subtribe and in other members of Heliantheae *s. str.*, representing most likely a synapomorphy for these genera. *Delilia* appears as basal in the group that includes the weedy monotypic *Synedrella*, the mainly Mexican *Lasianthaea* and *Schizoptera* from Ecuador and Mexico. Most plants of this group share a similar scarious and papery consistency of the inner phyllaries and pales. The inclusion of *Delilia* in Ecliptinae supports Robinson's view (1981) that this genus belongs in this subtribe and not in Milleriinae as suggested by Stuessy (1977).

Clade C. This clade contains species with cypselas having wings and a pappus of awns or squamellae elevated on a rostrum. These characteristics can be also seen in some genera of clade F. In the cpDNA analysis (Moraes *et al*. submitted), the great majority of the genera of clade C appeared combined in a major clade with most genera of clade F. The cpDNA results, the lack of support for most of the relationships depicted in clade C and the morphological similarity among the species of this clade with some of Clade F lead us to hypothesize that all these genera are probably a recent radiation in the New World tropics from a single ancestor.

The basal group that is resolved in clade C is composed by the shrubby monospecific genus *Trigonopterum*, endemic to Galápagos Islands, sister to *Sphagneticola*, a genus of four species common at lower elevations throughout the tropics, often near waterways or along the coast (Pruski, 1996). The affinities between these genera are strongly supported (100% bootstrap) and this corroborates results based on cpDNA data (Panero *et al.*, 1999; Moraes *et al.*, submitted). The origin of *Trigonopterum* in the Galápagos Islands was hypothesized by Panero *et al.* (1999) to be a long-distance dispersal event from a tropical American progenitor. Adapted to the dry habitats of the

Galápagos Islands, *Trigonopterum* differs from *Sphagneticola*, which is associated to wet or marshy coastal habitats, in many characters related to vegetative organs such as narrow leaves and a shrubby habit. On the other hand, these genera share a suite of floral characters including an urceolate involucre that become hemispheric in fruit; funnelform to campanulate corollas of the disc flowers; and strongly tuberculate cypselas in maturity, that are clavate to pyriform, attenuate toward the base; and finally, the pappus in these genera form a fimbriate, well developed crown.

We sampled three North American species of *Wedelia* out of twenty as recognized by Strother (1991). This auhor sorted them out into two groups. *Wedelia simsioides* was placed in the group of species that have been named in *Zexmenia*, characterized by fertile ray florets and strongly flattened, quadrate or weakly biconvex, usually winged cypselas. Plants of this group are associated with mesic to wet habitats, either restricted to mostly coastal habitats, or like *W. simsioides*, are narrowly distributed endemics closely associated with or restricted to wet or marshy habitats (Strother, 1991). The other group of wedelias have been mostly named in *Aspilia.* This group of plants is characterized by sterile ray florets, nearly pyriform or plumply biconvex, usually wingless cypselas (Strother, 1991), being found mostly above 1500 m, in relatively dry habitats. From this group we sampled *W. purpurea* and *W. tegetis* and found these two taxa to be sister to each other and not clustering with *W. simisioides*. This result, although not well supported, may be indicative of a non-monophyletic genus *Wedelia* and that the two groups recognized by Strother within *Wedelia* may represent phyletic lines with different evolutionary histories converging on some similarities of the cypsela. An understanding of the phylogenetic relationships of *Wedelia* and relatives will require extensive sampling across the Neotropical region and additional data.

The two species of *Oyedaea* sampled comprise a monophyletic group, which together with *Steiractinia*, *Wedelia*, *Elaphandra* Strother and *Zexmenia* form a strongly

supported clade with 100% bootstrap. The affinities among these genera agree with the results of cpDNA data (Panero *et al.*, 1999; Moraes *et al.*, submitted). A set of morphological characters is shared by these group of plants. The most obvious is the cypsela apex contracted to a short neck or rostrum; this character however appears in parallel once again, as it is also present in *Blainvillea*, member of clade F. The members of clade C share an involucre of mostly graduated phyllaries with the outer being proximally cartilaginous and distally herbaceous. In addition, these taxa have relatively large carpopodia at the base of their cypsela. This structure is composed by two shiny plates, and most cypselas in a head bear elaiosomes between the carpopodial plates (Strother, 1991). The only member of the cladein which these structures are very small or lacking is the genus *Elaphandra*. The type of the subtribe, *Eclipta*, is included in this clade. This relationship however, has no support.

Clade D. This clade is composed of the genera *Otopappus* and *Oblivia*. The species of these two genera are mostly distributed in Mexico and Central America and their close relationship has been widely accepted (Strother 1989b). Our results support the possibility of recognizing *Oblivia* as a distinct genus and disagree with the results from cpDNA restriction site analysis (Panero *et al.*, 1999), where *Oblivia* appears nested within *Otopappus* (the same DNA accessions were used in both analysis). The cpDNA results may reflect chloroplast transfer between lineages of *Otopappus* and *Oblivia* from past hybridization. *Oblivia* is similar to *Otopappus* in several ways. Both genera share cypselas narrowly oblanceolate or cuneate in outline and the pappus awns are borne on the apex of the cypsela, not raised on a rostrum. In addition, the cypsela wings extend to the awn bases in *Oblivia* and along the entire length of the awns in *Otopappus*

Clade E. This clade is comprised by the two species of *Jefea* sampled. The genus consists of five species, all transferred from *Zexmenia*, ranging from southern United States south and east through Mexico to Guatemala (Strother, 1991). *Jefea* resembles *Dimerostemma* in involucre composed by outermost phyllaries much like the foliage in shape, texture and indument.

Clade F. This clade is resolved in the strict consensus tree as sister to *Dimerostemma* and *Angelphytum* clade, but there is not support for this position. Clade F consist of two main subclades (Fig. 1). The first one contains the monotypic genus *Perymeniopsis*, endemic to central Mexico, as sister to *Rensonia*, also monotypic but from southern Mexico to Central America; and these two genera are collectively sister to *Clibadium*, a genus of approximately 40 species with its center of distribution in Central America. All these relationships have less than 50% bootstrap support. *Perymeniopsis* is not sister to nor conspecific with *Perymenium* (in the next subclade) as suggested by Turner (1988b). The most obvious character shared by *Perymeniopsis* and *Perymenium* is a pappus of deciduous bristles arranged more or less radially. This character is also shared by *Melanthera* and *Steiractinia*, the latter nested in clade C. Robinson (1981) minimized the importance of this pappus character in these genera and suggested that the pappus of *Perymeniopsis* is significantly different from any other genus in the Ecliptinae by having two whorls of bristles and squamellae inserted at a slightly higher level.

In the other main subclade, *Melanthera*, *Wollastonia* and *Lipochaeta* appear unresolved in a trichotomy and these genera are collectively sister to *Perymenium*. A close relationship between *Wollastonia biflora* with members of both sections of *Lipochaeta* sensu Gardner (1979) is also supported by sterile hybrids from crosses involving these taxa made by Rabakonandrianina & Carr (1981). The ITS and ETS data cannot provide an evaluation of the treatment of Wagner & Robinson (2001) in which

Wollastonia and *Lipochaeta* sect. *Aphanopappus* (n = 15, including *Lipochaeta integrifolia*) as delimited by Gardner (1979) are incorporated into *Melanthera*. In their treatment, they considered a more restricted delimitation of *Lipochaeta* to include only six allopolyploid species (n = 26) that corresponds to *Lipochaeta* sect. *Lipochaeta sensu* Gardner (1979).

The genus *Blainvillea* is a moderately supported member in clade F (bootstrap = 81%), whereas in a recent study using cpDNA data (Moraes *et al.* submitted) *Blainvillea* is basal to a clade strongly supported, containing *Lasianthaea* and the mostly ruderal species in Ecliptinae, as exemplified by *Synedrella*, *Delilia* and *Calyptocarpus* (all nested in clade B). This apparent incongruence may be the result of reticulate evolution in which the paternal parent is a member of Clade F and the maternal parent is potentially related to *Lasianthaea* and relatives.

***Dimerostemma/Angelphytum* clade**. The morphological difference between *Angelphytum* and *Dimerostemma* is in the peripheral or ray flower sexuality, sterile in *Dimerostemma*, fertile in *Angelphytum*. Except for this character, *Angelphytum* is essentially identical to *Dimerostemma* in all morphological characteristics. Our results show that *Dimerostemma* is paraphyletic with the exclusion of *Angelphytum* and the species of the two genera comprise a strongly supported group (Fig. 1). *Dimerostemma annuum* is sister to a clade with two main subclades. The first combines most *Angelphytum* species (in boldface, Fig. 1) and the other contain three species of *Angelphytum* (*A. arnotti*, *A. reitzii* and *A. goyazense*) clustered with the majority of *Dimerostemma* species. The species of *Angelphytum* do not form a monophyletic group, and the type of the genus (*A. matogrossense*) is basal to the clade containing the type species of *Dimerostemma* (*D. brasilianum*).

This result and the lack of enough morphological evidence for the division between the two genera has led us to propose the merging of *Angelphytum* in the synonymy of

Dimerostemma. Reflecting about the circumscription of *Angelphytum*, this view was also recently shared by the late G. M. Barroso (personal communication), the author of the genus *Angelphytum*. The discussion henceforth assumes an expanded genus *Dimerostemma* to include all species of *Angelphytum*. From here on the species that are presently being transferred from *Angelphytum* will be referred to *Dimerostemma*. The necessary nomenclatural combinations of *Angelphytum* into *Dimerostemma* are provided below. These transfers bring the total number of species in the genus to 29.

Dimerostemma is circumscribed by an involucre with an outer series of leaf-like phyllaries, peripheral (ray and outer disc) flowers fertile or sterile without style, disc corollas with cylindrical upper throats, style branches becoming strongly coiled after anthesis, and inner cypselas obovate in outline, cuneate toward base, mostly laterally flattened and typically winged on the margins. The pappus combines the most reliable features in distinguishing *Dimerostemma* among ecliptinous genera, probably representing its morphological apomorphy. The pappus of *Dimerostemma* is coroniform with awns mostly well developed that are distinct in being stout, triquetrous, tapering and continuous with the margins of the cypsela. *Dimerostemma* is the only member in the subtribe that is differentiated by the extension of phytomelanin from the body of the cypsela to the base of the awns. The crown is inserted directly on the apex of the cypsela body, not raised on a rostrum as in *Oyedaea*, *Zexmenia* and *Wedelia* (in clade C).

The basal taxon in this clade, *D. annuum*, is a rare, narrowly distributed endemic, restricted to calcareous soils of the border region between Brazil and Paraguay. The species is known only from two collection: the type from Paraguay and the other gathered on rocky shallow calcareous soils on the periodically inundated banks of a seasonal pond in the district of Bonito, Mato Grosso do Sul, southwestern Brazil.

Dimerostemma annuum has several unique traits for the group: a slender annual herb and pales slightly conduplicate, whereas the other species of *Dimerostemma* are

robust perennials and show pales strongly conduplicate, usually carinate-alate. Based on the nuclear tree, annual habit in Ecliptinae appears in parallelism four times, in the subclade of *Delilia* (within clade B, including *Synedrella* and *Schizoptera*) in *Blainvillea* and in *Baltimora* (members of clade F), and in *D. annuum* (Fig. 1). Evolution of annual habit in lineages of helenioid Heliantheae also appears to have evolved from ancestral perennial condition (Baldwin *et al.*, 2002)

All species in the first subclade, except *D. myrtifolium*, share similar shape of leaves, being mostly membranous, ovate, shortly attenuate at base, acuminate at apex. The relationship of *D. apense* from Mato Grosso do Sul and neigbouring Paraguay, *D. herzogii* from Bolivia, and *D. bahiense* from northeastern Brazil is further supported by similar shape of disc cypsela.

In the second subclade, despite of the sister relationship of *D. arnottii* and *D. reitzii* being weakly supported by bootstrap analysis, it is further supported morphologically by similar cypselas with well developed wings and awns. Some specimens of *D. arnotti* with short and narrow leaves are very similar to *D. reitzii* and the latter could be interpreted as belonging to the circunscription of *D. arnotti*, which is a widely dispersed polymorphic aggregate.

The next branch in the second subclade contains *D. grazielae* sister to *D. episcopale*. This relationship is strongly supported by bootstrap analysis. These species occur in a very similar but disjunct habitat, have the same shrubby habit, but unlike the other shrubby *Dimerostemma* species, both possess a xylopodium. Except for the phyllaries shape, they share all technical characters and may prove to be conspecific.

The relatively rare *D. humboldtianum* is basal to the branch containing the relatively common *D. lippioides*, *D. brasilianum* and *D. vestitum*. The latter three species occur frequently in Goiás and Minas Gerais, where they grow sympatrically and bloom at the same time. *Dimerostemma lippioides*, *D. brasilianum* and *D. vestitum* share with each

other broadly ovate to orbicular leaves, with a good portion of their specimens being easily separated from each other mainly by features of the cypsela. In this way, *D. vestitum* resembles *D. humboldtianum* in the cypselas having a tendency for showing longitudinal ridges and a thickened body which is rhombic in cross section. *Dimerostemma lippioides* resembles *D. brasilianum* in the cypselas being broadly winged with well developed awns. *Dimerostemma lippioides*, *D. brasilianum* and *D. vestitum*, however, form a species-complex with intermediate individuals among them. The molecular data support the affinities of these three species, and their variation in morphological features may be the result of hybridization.

Most species of *Dimerostemma* possess a xylopodium, which is an adaptation for the cerrado ecosystem with mostly acid soils, often with a high aluminum content. The presence or not of this structure do not seem to be indicative of a phylogenetic relationship. In the first clade, only *D. myrtifolium*, which grows in cerrado has xylopodium, all the remaining species in this clade do not have xylopodium and were found in dry-forest formation with calcareous soils (mata seca decídua). Most species in the second clade grow in the cerrado habitat and possess xylopodium, except *D. goyazense* and *D. bishopii*, both without xylopodium were found growing in mata seca decídua on calcareous soils. Within *Dimerostemma* clade, eradiate heads appear independently twice, in *A. matogrossense* and in *D. brasilianum* (in the latter the heads are mostly eradiate or with a few small rays in transition to tubular shape).

Likewise, the absence of wings in the disc cypsela does not appear to represent a phylogenetic relationship. *D. vestitum*, *D. bishoppii*, and *D. species nova* share with each other thickened subquadrangular cypselas, which are wingless or with wings much reduced, but as this three species are found scattered in *Dimerostemma* clade, this obvious morphological feature does not seem to correspond to a synapomorphy.

TAXONOMIC IMPLICATIONS

To formalize the transfer of *Angelphytum* into *Dimerostemma*, the following new combinations are required (the combinations proposed in this thesis will be valid published in a near future somewhere else):

Dimerostemma apense (Chodat) M. D. Moraes, comb. nov. Basionym: *Aspilia apense* Chodat, Bull. Herb. Boissier sér. 2 (3): 721. 1903.

Dimerostemma arnottii (Baker) M. D. Moraes, comb. nov. Basionym: *Verbesina arnottii* Baker in Martius, Fl. bras. 6 (3): 215. 1884.

Dimerostemma aspilioides (Griseb.) M. D. Moraes, comb. nov. Basionym: *Verbesina aspilioides* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 194. 1879.

Dimerostemma bahiense (H. Rob.) M. D. Moraes, comb. nov. Basionym: *Angelphytum bahiense* H. Rob., Proc. Biol. Soc. Wash. 97 (4): 966. 1984.

Dimerostemma goyazense (Gardner) M. D. Moraes, comb. nov. Basionym: *Lipochaeta goyazensis* Gardner, Lond. J. Bot. 7: 406. 1948.

Dimerostemma grisebachii (Baker) M. D. Moraes, comb. nov. Basionym: *Verbesina grisebachii* Baker in Martius, Fl. bras. 6.(3): 214. 1884.

Dimerostemma hatschbachii (H. Rob.) M. D. Moraes, comb. nov. Basionym: *Angelphytum hatschbachii* H. Rob., Proc. Biol. Soc. Wash. 97 (4): 967. 1984.

Dimerostemma herzogii (Hassl.) M. D. Moraes, comb. nov. Basionym: *Zexmenia herzogii* Hassl., Repert. Spec. Nov. Regni Veg. 7: 357. 1909.

Dimerostemma hieronymi (Hassl.) M. D. Moraes, comb. nov. Basionym: *Zexmenia hieronymi* Hassl., Repert. Spec. Nov. Regni Veg. 14: 157. 1915.

Dimerostemma indutum (Chodat) M. D. Moraes, comb. nov. Basionym: *Aspilia induta* Chodat, Bull. Herb. Boissier sér. 2 (3): 720. 1903.

Dimerostemma matogrossense (G. M. Barroso) M. D. Moraes, comb. nov. Basionym: *Angelphytum matogrossense* G. M. Barroso, Bol. Soc. Argent. Bot. 19 (1-2) 9. 1980.

Dimerostemma myrtifolium (Chodat) M. D. Moraes, comb. nov. Basionym: *Verbesina myrtifolia* Chodat, Bull. Herb. Boissier sér. 2 (2): 393. 1902.

Dimerostemma oppositifolium (A. A. Sáenz) M. D. Moraes, comb. nov. Basionym: *Zexmenia oppositifolia* A. A. Sáenz, Hickenia 1(54): 285. 1982.

Dimerostemma paraguariense (Chodat) M. D. Moraes, comb. nov. Basionym: *Verbesina paraguariensis* Chodat, Bull. Herb. Boissier sér. 2 (3): 722. 1984.

Dimerostemma pseudosilphoides (Hassl.) M. D. Moraes, comb. nov. Basionym: *Zexmenia pseudosilphioides* Hassl., Repert. Spec. Nov. Regni Veg. 14: 263. 1916.

Dimerostemma reitzii (H. Rob.) M. D. Moraes, comb. nov. Basionym: *Angelphytum reitzii* H. Rob., Proc. Biol. Soc. Wash. 97 (4): 968. 1984.

Dimerostemma tenuifolium (Hassl.) M. D. Moraes, comb. nov. Basionym: *Zexmenia tenuifolia* Hassl., Repert. Spec. Nov. Regni Veg. 14: 178. 1915.

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Table 1. List of specimens of Asteraceae sequenced in this study. Voucher specimens are deposited at TEX and/or UEC. Genbank accession numbers are as follows: ITS; ETS. NS = no sequence available.

Baltimora recta L.; Mexico: Chiapas. *Panero 4487* (TEX); GenBank nos. AY303403, AY303465. ***Blainvillea rhomboidea*** Cass.; Brazil: Sao Paulo. *Moraes 657* (UEC); GenBank nos. AY303404, AY303466. ***Calyptocarpus vialis*** Less.; Mexico: Nuevo León. *Panero 2342* (TEX); GenBank nos. AY303405, AY303467. ***Clibadium alatum*** H. Rob.; Ecuador: Carchi. *Panero 3039* (TEX); GenBank nos. AY303406, AY303468. ***Damnxanthodium calvum*** (Greenm.) Strother; Mexico: Durango. *Panero 2252* (TEX); GenBank nos. AY303407, AY303469. ***Delilia biflora*** (L.) Kuntze; Mexico: Guerrero. *Panero 2327* (TEX); GenBank nos. AY303413, AY303475. ***Dimerostemma annuum*** (Hassl.) H. Rob.; Brazil: Mato Grosso do Sul. *Moraes 629* (UEC); GenBank nos. AY303408, AY303470. ***Dimerostemma apense*** (Chodat) M. D. Moraes; Brazil: Mato Grosso do Sul. *Moraes 557* (UEC); GenBank nos. AY303391, AY303453. ***Dimerostemma arnottii*** (Baker) M. D. Moraes; Brazil: Parana. *Moraes 435* (UEC); GenBank nos. AY303392, AY303454. ***Dimerostemma lippioides*** (Baker) S. F. Blake; Brazil: Goias. *Moraes 581* (UEC); GenBank nos. AY303409, AY303471. ***Dimerostemma lippioides*** (Baker) S. F. Blake; Brazil: Goias. *Moraes 378* (UEC); GenBank nos. AY303410, AY303472. ***Dimerostemma bahiense*** (H. Rob.) M. D. Moraes; Brazil: Bahia. *Moraes 447* (UEC); GenBank nos. AY303394, AY303456. ***Dimerostemma bishopii*** H. Rob.; Brazil: Goias. *Moraes 640* (UEC); GenBank nos. AY303411, AY303473. ***Dimerostemma brasilianum*** Cass.; Brazil: Goias. *Moraes 649* (UEC); GenBank nos. AY303412, AY303474. ***Dimerostemma episcopale*** (H. Rob.) H. Rob.; Brazil: Bahia. *Moraes 454* (UEC); GenBank nos. AY303414, AY303476. ***Dimerostemma goyazense*** (Gardner) M. D. Moraes; Brazil: Goias. *Moraes 636* (UEC); GenBank nos. AY303395,

AY303457. ***Dimerostemma grazielae*** H. Rob.; Brazil: Goias. *Moraes 647* (UEC); GenBank nos. AY303415, AY303477. ***Dimerostemma herzogii*** (Hassl.) M. D. Moraes; Bolivia. *Nee 48071* (NY); GenBank nos. AY303396, AY303458. ***Dimerostemma humboldtianum*** (Gardner) H. Rob.; Brazil: Goias. *Moraes 540* (UEC); GenBank nos. AY303416, AY303478. ***Dimerostemma matogrossense*** (G. M. Barroso) M. D. Moraes; Brazil: Goias. *Batalha 4027* (UEC); GenBank nos. AY303397, AY303459. ***Dimerostemma myrtifolium*** (Chodat) M. D. Moraes; Brazil: Mato Grosso do Sul. *Moraes 619* (UEC); GenBank nos. AY303398, AY303460. ***Dimerostemma pseudosilphioides*** (Hassl.) H. Rob.; Brazil: Mato Grosso do Sul. *Moraes 634* (UEC); GenBank nos. AY303399, AY303461. ***Dimerostemma reitzii*** H. Rob.; Brazil: Santa Catarina. *Moraes 427* (UEC); GenBank nos. AY303400, AY303462. ***Dimerostemma species nova*** ; Brazil: Mato Grosso do Sul. *Moraes 613* (UEC); GenBank nos. AY303417, AY303479. ***Dimerostemma vestitum*** (Baker) S. F. Blake; Brazil: Goias. *Moraes 372* (UEC); GenBank nos. AY303419, AY303481. ***Eclipta prostrata*** (L.) L.; USA: Texas, Travis Co.. *Panero 2345* (TEX); GenBank nos. AY303421, AY303483. ***Elaphandra paucipunctata*** H. Rob.; Ecuador: El Oro. *Panero 2991* (UEC); GenBank nos. AY303422, AY303484. ***Idiopappus quitensis*** H. Rob. & Panero; Ecuador: Pichincha. *Panero 3008* (TEX); GenBank nos. AY038116 (ITS1), AY038149 (ITS2), AY038083. ***Jefea lantanifolia*** (S. Schauer) Strother; Mexico: San Luis Potosi. *Panero* (TEX); GenBank nos. AY303423, AY303485. ***Jefea pringlei*** (Greenm.) Strother; Mexico: Puebla. *Panero 2311* (TEX); GenBank nos. AY303424, AY303486. ***Kingianthus paniculatus*** (Turcz.) H. Rob.; Ecuador: Tungurahua. *Panero 2900* (TEX); GenBank nos. AY303425, AY303487. ***Kingianthus paradoxus*** H. Rob.; Ecuador: Azuay. *Panero 2953* (TEX); GenBank nos. AY303426, AY303488. ***Lasianthaea helianthoides*** DC.; Mexico: Guerrero. *Panero* (TEX); GenBank nos. AY303427, AY303489. ***Lipochaeta integrifolia*** A Gray; USA: Hawaii collected by S. Keeley (no voucher); GenBank nos. AY303428, AY303490.

Lundellianthus breedlovei (B. L. Turner) Strother; Mexico: Chiapas. *Panero 3112* (TEX); GenBank nos. AY303429, AY303491. ***Lundellianthus jaliscensis*** (McVaugh) Strother; Mexico: Jalisco. *Panero 3153* (TEX); GenBank nos. AY303430, AY303492. ***Melanthera nivea*** Small; Mexico: Chiapas. *Panero 2519* (TEX); GenBank nos. AY303431, AY303493. ***Monactis pallatangensis*** (Hieron.) H. Rob.; Ecuador: Chimborazo. *Panero 2907* (TEX); GenBank nos. AY303432, AY303494. ***Montanoa atriplicifolia*** H. Rob.; Mexico: Oaxaca. *Panero 2715* (TEX); GenBank nos. AY038119 (ITS1), AY038152 (ITS2), AY038036. ***Oblivia mikanioides*** (Britton) J. L. Strother; Venezuela: Aragua. *Panero 2621* (TEX); GenBank nos. AY303433, AY303495. ***Otopappus epaleaceus*** Hemsl.; Mexico: Guerrero. *Panero 2515* (TEX); GenBank nos. AY303434, AY303496. ***Otopappus verbesinoides*** Benth.; Mexico: Chiapas. *Panero 3125* (TEX); GenBank nos. AY303435, AY303497. ***Oyedaea jahnii*** S. F. Blake; Venezuela: Merida. *Panero 2691* (TEX); GenBank nos. AY303436, AY303498. ***Oyedaea verbesinoides*** DC.; Venezuela: Aragua. *Panero 2609* (TEX); GenBank nos. AY303437, AY303499. ***Perymeniopsis ovalifolia*** (A. Gray) H. Rob.; Mexico: Tamaulipas. *Panero 2380* (TEX); GenBank nos. AY303438, AY303500. ***Perymenium ecuadoricum*** S. F. Blake; Ecuador: Chimborazo. *Panero 2911* (TEX); GenBank nos. AY303439, AY303501. ***Perymenium macrocephalum*** Greenm.; Mexico: Guerrero. *Panero 2274* (TEX); GenBank nos. AY303440, AY303502. ***Rensonia salvadorica*** S. F. Blake; Mexico: Chiapas. *Panero 2532* (TEX); GenBank nos. AY303441, AY303503. ***Rojasianthe superba*** Standley & Steyermark; Mexico: Chiapas. *Panero 2892* (TEX); GenBank nos. AF171947(ITS1), AF171986 (ITS2), AF172025. ***Schizoptera peduncularis*** (Benth.) S. F. Blake; GenBank nos. AF465887 (Rauscher, J.T. 2002), NS. ***Sphagneticola trilobata*** (L.) J. F. Pruski; Venezuela: Portuguesa. *Panero 2639* (TEX); GenBank nos. AY303442, AY303504. ***Steiractinia sodiroi*** (Hieron.) S. F. Blake; Ecuador: Bolívar. *Panero 2993* (TEX); GenBank nos. AY303443, AY303505. ***Synedrella nodiflora*** (L.) Gaertn.; Venezuela: Aragua. *Panero 2612* (TEX); GenBank nos. AY303444,

AY303506. ***Tilesia baccata*** (L.) J. F. Pruski; Venezuela: Aragua. *Panero 2610* (TEX); GenBank nos. AY303445, AY303507. ***Trigonopterum laricifolium*** (Hook. f.) W. L. Wagner & H. Rob.; cultivated at Gotheburg University from seeds collected in the Galápagos Islands. (no voucher); GenBank nos. AY303446, AY303508. ***Verbesina myriocephala*** Sch. Bip.; Venezuela: Trujillo. *Panero 2656* (TEX); GenBank nos. AF171983 (ITS1), AF172022 (ITS2), AF172061. ***Wamalchitamia aurantiaca*** (Klatt) Strother; Costa Rica: Guanacaste. *Panero 2719* (TEX); GenBank nos. AY303447, AY303509. ***Wedelia purpurea*** (Greenm.) B. L. Turner; Mexico: Guerrero. *Panero 2296* (TEX); GenBank nos. AY303448, AY303510. ***Wedelia simsioides*** McVaugh; Mexico: Nayarit. *Panero 2231* (TEX); GenBank nos. AY303449, AY303511. ***Wedelia tegetis*** Strother; Mexico: Durango. *Panero 2625* (TEX); GenBank nos. AY303450, AY303512. ***Wollastonia biflora*** (L.) DC.; USA: Hawaii. collected by S. Keeley in Waimea Falls Park, accession number 75-165 (no voucher); GenBank nos. AY303451, AY303513. ***Zexmenia serrata*** La Llave & Lex.; Mexico: Oaxaca. *Panero 2765* (TEX); GenBank nos. AY303452, AY303514.

Figure 1. Strict consensus tree based on ITS and ETS sequence data of subtribe Ecliptinae, including *Dimerostemma* lineage, and three outgroups. The species that are presently being transferred from the genus *Angelphytum* to *Dimerostemma* are in boldface. Bootstrap support is given on the branches for values > 50%. The cladogram has 2088 steps, CI = 0.423 (excluding uninformative characters) and RI = 0.722.

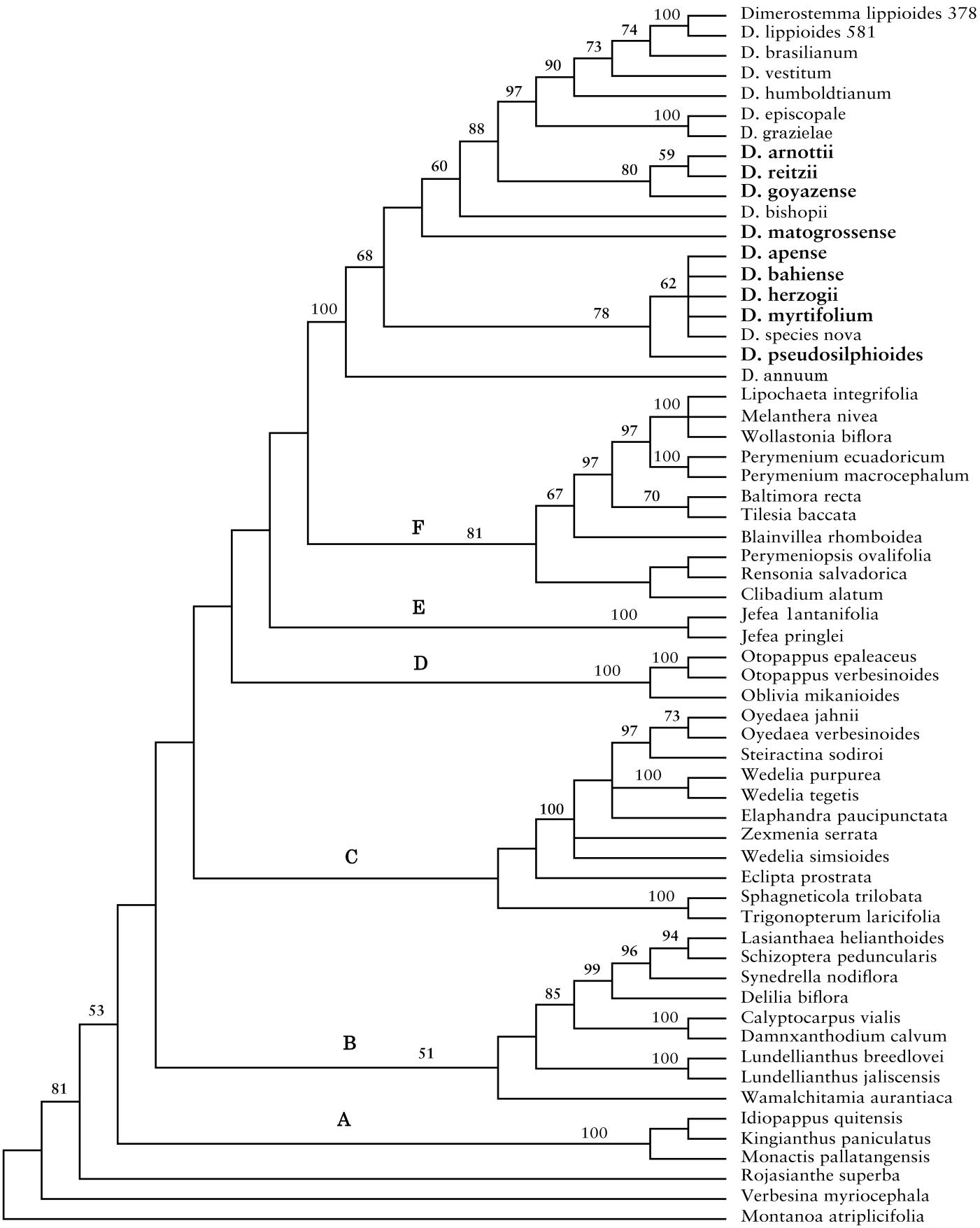
Dimerostemma lippioides 378
D. lippioides 581
D. brasilianum
D. vestitum
D. humboldtianum
D. episcopale
D. grazielae
D. arnottii
D. reitzii
D. goyazense
D. bishopii
D. matogrossense
D. apense
D. bahiense
D. herzogii
D. myrtifolium
D. species nova
D. pseudosilphioides
D. annuum
Lipochaeta integrifolia
Melanthera nivea
Wollastonia biflora
Perymenium ecuadoricum
Perymenium macrocephalum
Baltimora recta
Tilesia baccata
Blainvillea rhomboidea
Perymeniopsis ovalifolia
Rensonia salvadorica
Clibadium alatum
Jefea lantanifolia
Jefea pringlei
Otopappus epaleaceus
Otopappus verbesinoides
Oblivia mikanioides
Oyedaea jahnii
Oyedaea verbesinoides
Steiractina sodiroi
Wedelia purpurea
Wedelia tegetis
Elaphandra paucipunctata
Zexmenia serrata
Wedelia simsioides
Eclipta prostrata
Sphagneticola trilobata
Trigonopterum laricifolia
Lasianthaea helianthoides
Schizoptera peduncularis
Synedrella nodiflora
Delilia biflora
Calyptocarpus vialis
Damnxanthodium calvum
Lundellianthus breedlovei
Lundellianthus jaliscensis
Wamalchitamia aurantiaca
Idiopappus quitensis
Kingianthus paniculatus
Monactis pallatangensis
Rojasianthe superba
Verbesina myriocephala
Montanoa atriplicifolia
A
B
C
D
E
F

Figure 1.

Capítulo 3: a ser submetido à revista Brittonia

The Brazilian *Dimerostemma* (Asteraceae: Heliantheae - Ecliptinae), with a new species and taxonomic adjustments

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Key words: *Dimerostemma*, Asteraceae, Heliantheae, Ecliptinae, Brazil.

ABSTRACT

Dimerostemma as circumscribed here includes the taxa recently known as *Angelphytum*. Nineteen species of *Dimerostemma*, endemic or occurring in Brazil are recognized. One new species (*Dimerostemma specie nova*) discovered in the Pantanal of Mato Grosso do Sul is described, illustrated and discussed; synonymies are proposed; and a combination (*D. oblongum*) is validated. Brazil with 19 of the current known species (approximately 80% of the total) is the principal focus of diversity for the genus. The greatest concentration of species is in the cerrado and campo rupestre of the central western Brazil. *Dimerostemma* is unified by its involucre with an outer series of leaf-like phyllaries and by an unconstricted coroniform pappus with awns mostly well developed, stout, triquetrous and continuous with the margins of the cypsela. It is specially differentiated by the extension of phytomelanin from the body of the cypsela to the base of the awns. The variation in the shape of leaves, outer phyllaries, pales tip and inner cypsela body; the presence or not of awns and their relative length; the development of crown and its margins are all diagnostic in species identification. A key to the Brazilian members of *Dimerostemma*, synonymies, descriptions, illustration and commentaries are provided, as well as notes on distribution, habitat, phenology and specimen citations.

INTRODUCTION

Dimerostemma Cass. is a genus endemic to South America with the highest concentration of species found in central-western Brazil. It is classified in tribe Heliantheae subtribe Ecliptinae as emended by Panero et al. (1999) as it possess mostly opposite leaves, foliaceous phyllaries and variously winged cypselas.

A hundred years after the description of *Dimerostemma* by Cassini (1817) with *D. brasilianum* as its only member, Blake (1917) emended the genus to include species from the genus *Oyedaea* DC. that lacked squamellae in their pappus. Under Blake's treatment, the genus *Dimerostemma* consisted of six species. Robinson (1984a) continued to rearrange the species of *Oyedaea* by placing in *Dimerostemma* all the remaining Brazilian species, leaving within *Oyedaea* species bearing a rostrum at the apex of the cypsela and mostly restricted to the Andes of northern South America. These additions to *Dimerostemma* raised the number in the genus to a total of eleven species.

Angelphytum, a genus established by Barroso (1980), has a similar taxonomic history. It was also originally monotypic and its circumscription was also expanded mainly by the transfer from a poorly defined genus (in this case from *Zexmenia* La Llave & Lex.). In the same year that the redelimitation of *Dimerostemma* was published by Robinson (1984a), this author in the same journal transferred to *Angelphytum* all the Brazilian species with radiate heads that have been previously placed in *Zexmenia* (Robinson,1984b). In this paper, the generic limits of *Angelphytum* were expanded to include a total of 14 species.

As remarked by Robinson (1984b), *Angelphytum* is related to *Dimerostemma*, which it resembles in herbaceous habit with a xylopodium in most species, disc corollas with cylindrical upper throats and contorted usually abaxially glanduliferous branches of styles, and variously winged cypselas not constricted at the apex. *Angelphytum* differs in

fertile peripheral flowers and in undifferentiated or irregularly differentiated outer phyllaries, which in *Dimerostemma* is respectively sterile and well differentiated.

To elucidate the inter - and infrageneric relationships of *Dimerostemma* and *Angelphytum*, a phylogenetic study based on ITS and ETS sequence data for the majority of the members of the mostly Neotropical subtribe Ecliptinae (Asteraceae: Heliantheae) was constructed by Moraes, Panero & Semir (in prep.). In this study, the nine species of *Dimerostemma* and nine species of *Angelphytum* sampled appear as a monophyletic group strongly supported. This clade is resolved in the strict consensus tree as sister to a grouping of mostly North American Ecliptinae and contain three main groups. The only annual species of the group, *Dimerostemma annuum* is basal to two main subclades containing each a combination of species of both genera. This result led the authors to consider *Angelphytum* as synonym of *Dimerostemma* and therefore to transfer all species of *Angelphytum* to *Dimerostemma.*

Dimerostemma as now recognized, including the taxa recently known as *Angelphytum*, contains 25 species. The Brazilian *Dimerostemma* consist of 19 species, including one that is newly described here. With approximately 80% of the current known species, Brazil is the principal center of diversity for *Dimerostemma*, with various endemic species. The region with greatest number of species is the campo rupestre and cerrado of central-western Brazil. The six species that have not been collected in Brazil and therefore are not treated here are: *D. asperatum* S. F. Blake and *D. herzogii* (Hassl.) H. Rob. (both restricted to Bolivia), *D. aspilioides* (Griseb.) H. Rob. and *D. indutum* (Chodat) H. Rob. (distributed in Argentina, Bolivia and Paraguay), *D. grisebachii* (Baker) H. Rob. (ocorring in Argentina, Paraguay and Uruguay) and *D. tenuifolium* (distributed in Argentina and Paraguay).

Dimerostemma is characterized by an involucre with an outer series of leaf-like phyllaries, disc corollas with cylindrical upper throats, style branches becoming strongly

coiled after anthesis, and by inner cypselas obovate in outline, cuneate toward base, usually laterally flattened and mostly winged on the margins. The pappus combines the most reliable features in distinguishing *Dimerostemma* among ecliptinous genera, probably representing its morphological apomorphy. The pappus of *Dimerostemma* is coroniform with awns mostly well developed that are distinct in being stout, triquetrous, tapering and continuous with the margins of the cypsela. *Dimerostemma* is the only member in the subtribe that is differentiated by the extension of phytomelanin from the body of the cypsela to the base of the awns. The crown is inserted directly on the apex of the cypsela body, not raised on a rostrum as in *Oyedaea*, *Zexmenia* and *Wedelia*.

The variation in the shape of leaves (Fig. 1), outer phyllaries (Fig. 2), pales tip that ranges from rounded, subulate or rigid pungent and inner cypselas body that are either laterally flattened associated with wings or subquadrangular and wingless (Fig. 3) are all valuable in characterizing species. The pappus, so important for the delimitation of the genus, aggregates diagnostic features in species identification as well. Awns are longer than the cypsela body, reduced to tooth like projection or missing. The crown between awns are relatively well developed or reduced to a ciliate or entire margin (Fig. 3).

Taxonomic Treatment

Dimerostemma Cass., Bull. Soc. Philom. 1817. TYPE: *Dimerostemma brasilianum* Cass.

Serpaea Gardner, London J. Bot. 7: 296. 1848. TYPE: *Serpaea ovata* Gardner [= *Dimerostemma brasilianum* Cass.].

Oyedaea DC. Subg. *Serpaea* (Gardner) Baker, in C. Martius, Fl. Bras. 6 (3): 206. 1884. TYPE: not designated, but including *Oyedaea vestita* Baker [= *Dimerostemma vestitum* (Baker) S. F. Blake], *O. ovata* (Gardner) Benth. [= *Dimerostemma brasilianum* Cass.], *Oyedaea lippioides* Baker [= *Dimerostemma lippioides* (Baker) S. F. Blake], *Oyedaea rotundifolia* Sch. Bip ex Baker [= *Dimerostemma brasilianum* Cass.].

Angelphytum G. M. Barroso, Bol. Soc. Argent. Bot. 19: 9. 1980. TYPE: *Angelphytum matogrossense* G. M. Barroso [= *Dimerostemma retifolium* (Sch. Bip.) S. F. Blake].

Basally woody *herbs* or *subshrubs*, annual (only one species = *D. annuum*) or mostly perennials, erect from a xylopodium or a woody caudex. *Leaves* opposite, sometimes alternate distally, proximally or throughout, broadly ovate to suborbicular on distinct petioles to linear and subsessile, gland-punctate abaxially, 3-nerved from near to well above the base (always 3-nerved from the base in *D. lippioides* and one-nerved in *D. reitzii* and *D. annuum*), mostly subpinnately netted to reticulate distally. *Heads* in loose dichasiiform associations of 2-3 at the ends of primary and axillary shoots (always solitary in *D. humboldtianum*, sometimes in *D. vestitum*). *Involucres* broadly campanulate (subglobose in *D. brasilianum*); *phyllaries* in ca. 3-4 series, the outer spreading (mostly erect in *D. oblongum*), much like the leaves in form and indument, the inner appressed, indurate at the base and foliaceous at the tip, more scarious toward the center of the head. *Receptacle* convex; *pales* mostly stramineous, surpassing the involucre before and after anthesis, conduplicate, variously carinate-alate (slightly conduplicate and not carinate-alate on *D. annuum*), falcate in outline, persistent, scarious, tips rounded to subulate or rigid pungent. *Ray florets* sterile lacking styles or pistillate and fertile (wanting in *D. retifolium* and sometimes in *D. brasilianum*); corollas liguliform, yellow, lamina oblong to elliptic or obovate, gland-punctate and mostly sparsely setulose abaxially. *Disc florets* perfect, fertile; corollas tubular, yellow, tube much shorter than the cylindrical to cylindrical-funnelform throat, lobes 5, deltate, minutely papillate adaxially, gland-punctate and mostly sparsely setulose abaxially, slightly thickened at tip; *anther thecae* blackish, connective and appendages stramineous, appendages deltate and gland-punctate abaxially, collars thickened, constricted at base and then narrowed; *style branches* stout, strongly coiled after anthesis, often gland-punctate abaxially, pillose distally, appendages short, acute to acuminate, ending with a few trichomas. *Cypselas* obovate in outline, cuneate toward

base, usually tuberculate on the faces, mostly winged, wings narrow to as broad as the body or lacking, the peripheral (ray and outer disc) mostly trigonous, usually 3-winged and 3-awned, the inner laterally flattened or sometimes thickened, subquadrangular, mostly 2-winged and 2-awned. *Pappus* coroniform, awns with phytomelanin extending from the body of the cypselas to its base, well developed, stout, trigonous, very broad to relatively narrow at base, tapering, sometimes reduced to tooth like projection or lacking, crown between awns not constricted, fragile, lacerate to erose or laciniate to fimbriolate, reduced to a ciliate or entire margin.

Dimerostemma ("two parted crown") is named for the longish stout and basally broad awns as seen in the type species.

Key to species of *Dimerostemma* native to Brazil

1. Ray florets absent or heads with a few small rays in transition to tubulate, less than 10 mm long, or rarely with deeply cleft linear laminas.

    2. Leaves opposite throughout or sometimes alternate distally; *blades* subchartaceous, broadly ovate to orbicular, rounded to truncate to subcordate at base, adaxial surface subtomentose or sometimes pilose-strigillose, the abaxial tomentose. Relatively abundant in Minas Gerais and Goiás ..... *D. brasilianum*

    2. Leaves alternate; *blades* coriaceous, elliptic to oblong-elliptic or sometimes ovate, cuneate at base, both surfaces appressed and densely scabridulous. Relatively rare in Mato Grosso do Sul and adjacent Goiás ..... *D. retifolium*

1. Ray florets with well developed laminas, mostly longer than 10 mm, if with deeply cut lobes, then elliptic to obovate never linear.

    3. Leaf blades broadly ovate or broadly elliptic to orbicular, if ovate, then rounded or obtuse at apex and rounded to truncate or cordate to subcordate at base.

4. Leaves mostly opposite, both surfaces mostly hispidulous, usually asperous to the touch, always 3-nerved from the base; *peduncles* mostly elongated and leafless; *cypselas* laterally flattened, mostly with smooth faces, without ridges, broadly winged.....*D.lippioides*

4. Leaves mostly alternate, both surfaces mostly tomentose to subtomentose, usually soft to the touch, 3-nerved from near to well above the base; *peduncles* mostly with leaves nearly or at the bases of the heads; *cypselas* thickened, subquadrangular, with 1(-3) longitudinal ridges, wingless or wings reduced to a narrow, often paler margins ..... *D. vestitum*

3. Leaf blades very narrowly oblong-elliptic or narrowly lanceolate to linear, oblong to elliptic or lanceolate to obovate, if ovate, then shortly acuminate to acute at apex. When obtuse at apex, then shortly attenuate to cuneate at base.

5. Leaf blades very narrowly oblong-elliptic or narrowly lanceolate to linear.

6. Slender annual herbs; *ray florets* sterile; *pales* sligthly conduplicate, not carinate-alate .....*D. annuum*

6. Basally woody perennial herbs or subshrubs, from a xylopodium; *ray florets* fertile; *pales* conduplicate, variously carinate-alate.

7. Leaf blades up to 2.7 cm long, one-nerved, not subpinnately netted distally or throughout, scabrous; *pappus awns* mostly unequal, the longest ca. of the same length of the cypsela body or longer..... *D. reitzii*

7. Leaf blades never shorter than 3 cm, 3-nerved, subpinnately netted distally or throughout, strigillose to velutinous to densely sericeous; *pappus awns* mostly subequal, the longest shorter, but not less than 3/4 the cypsela body length.....*D. arnottii*

5. Leaf blades lanceolate, oblong, elliptic, obovate, ovate or broadly ovate.

8. Cypselas (peripheral and inner) thickened, subquadrangular, wingless or with wings much reduced to a narrow margin; *pappus* mostly awnless, crown reduced to an entire, minutely erose or ciliate margin.

9. Leaf blades rounded to truncate or subcordate at base .....*D. bishopii*

9. Leaf blades shortly attenuate at base.

10. Branches brownish-green; *leaf length* 2 times width, with serrate margins and abaxial surface strigillose .....*D. species nova*

10. Branches stramineous; *leaf length* 3-5 times width, with remotely serrulate margins and abaxial surface densely villous .....*D. virgosum*

8. Cypselas the inner laterally flattened or sometimes slightly thickened, mostly winged; *pappus* with awns reduced to tooth like projections or much longer, if awnless, then with crown 0.2-0.8 mm high or higher, partially or almost completely fused to the cypsela body, with entire or laciniate to fimbriolate or lacerate margins.

11. Ray florets sterile.

12. Stems with vegetative shoots distally at the base of the peduncles; *leaf blades* submembranous, drying conduplicate and thus becoming falcate shaped, both surfaces with trichomes so small, apressed and sparse that the blades appear subglabrate, rarely both surfaces pilose.....*D. humboldtianum*

12. Stems without vegetative shoots distally at the base of the peduncles; *leaf blades* coriaceous or subcartaceous, rigid, the abaxial surface densely strigose or tomentose to villous.

13. Leaf blades coriaceous, rigid; *outer phyllaries* mostly smaller than the inner, erect, rounded and mucronulate at apex. Restricted to Minas Gerais .....
.....*D. oblongum*

13. Leaf blades subchartaceous; *outer phyllaries* mostly much longer than the inner, spreading, acute to very shortly acuminate or obtuse at apex. Chapada Diamantina, Bahia and Chapada dos Veadeiros, Goiás.

14. Phyllaries the outer mostly linear or with a long linear base up to 1.5 mm wide; *pales* with mostly purple, triangular, rigid and acute tip; *ray florets* with laminas mostly purplish or yellowish with purple veins, shallowly cut lobes or entire at apex. Endemic to Chapada dos Veadeiros in east-central Goiás
.....*D. grazielae*

14. Phyllaries the outer broader, 2-8 mm wide; *pales* with mostly stramineous, rounded to obtuse or sometimes deltate (1: 1 l/w) tip; *ray florets* with laminas mostly yellow, with deeply cut lobes. Endemic to Chapada Diamantina, near Rio de Contas, Bahia ..... *D. episcopale*

11. Ray florets fertile.

15. Pappus of inner cypselas with the longest awns ca. of the same or not less than ¾ the cypsela body length.

16. Leaf blades subcoriaceous, both surfaces appearing subglabrate as the trichomes are so small, appressed, sparsely and minutely scabridulous; *cypselas* 2.5-3 mm wide ..... *D. myrtifolium*

16. Leaf blades submembranous, both surfaces strigillose to velutinous to densely sericeous; *cypselas* up to 2 mm wide .....*D. arnottii*

15. Pappus of inner cypselas with awns reduced to tooth like projection or the longest less than ¾ the cypsela body length or sometimes awnless.

17. Pales 9-10 mm long, with rigid, linear and pungent tip up to 3.5 mm long. .....*D. apense*

17. Pales 7-9 mm long, with deltate (ca. 1 x 1 mm), subulate or triangular tip up to 2 mm long.

18. Pales with deltate (ca. 1 x 1 mm) tip; *pappus* with crown almost totally fused to the cypsela body (mostly more than 2/3). Restricted to Bahia..... .....*D. bahiense*

18. Pales with subulate or triangular tip up to 2 mm long; *pappus* with crown partially fused to the cypsela body (less than 1/3).

19. The inner cypsela wingless or mostly asymetrically winged with wings wider on the opposite side of pale; *pappus* mostly one-awned or awnless. Occuring in Goiás and adjacent Minas Gerais ....*D. goyazense*

19. The inner cypsela symmetrically winged, obscurely ciliate distally on the opposite side of pale; *pappus* 2-awned. Distributed in Mato Grosso do Sul and neighbouring Paraguay ..... *D. pseudosilphioides*

Dimerostemma annuum (Hassl.) H. Rob., Proc. Biol. Soc. Wash. 97 (3): 621. 1984. *Oyedaea annua* Hassl., Repert. Spec. Nov. Regni Veg. 14: 175. 1915. TYPE: PARAGUAY. In campis rupestribus calcareis in regione collis Margarita, Mar 1912/13, *E. Hassler 11030* (HOLOTYPE: G; ISOTYPES: BM, NY, K-n.v., photos: F, photo-K at UEC). (Fig. 1 R, Fig. 2 G, Fig. 3 A)

Slender, *annual herbs* up to 60 cm high. *Leaves* opposite, subsessile or with *petioles* up to 5 mm long; *blades* 4.5-6.5 x 0.3-0.5 cm, submembranous, linear to very narrowly oblong-elliptic, attenuate at base, acute to shortly acuminate at apex, margins entire or obscurely toothed, adaxial surface with trichomes so small, appressed and sparse that appear subglabrate, the abaxial sparsely and appressed strigillose, one-nerved. *Phyllaries* the outer 6-22 x 1.5-3 mm, linear to lanceolate, the inner 4-5 x 3-3.5 mm, broadly ovate, shortly acuminate to acute at the apex. *Pales* 4-5 x ca. 0.5 mm when folded, slightly conduplicate, not carinate-alate, with subulate or triangular tip up to ca. 0.5 mm long. *Ray florets* sterile, tube 0.5-1 mm long, lamina 7.5-16 x 3.5-6 mm, oblong to obovate, glabrous. *Disc florets* with corollas 2.8-3 mm long, lobes glabrous. *Cypselas* 2.2-2.8 x 1-1.3 mm, thickened, subquadrangular, wings up to 0.8 mm wide, the peripheral wingless, densely tuberculate with maturity; *pappus* with awns reduced to tooth like projections or less than one half of the cypsela body or awnless, crown 0.2-0.4 mm high, partially fused to the body (less than 1/3), with minutely erose margins.

Distribution, habitat and phenology: Known from the type location in Paraguay. Also from the adjacent state of Mato Grosso do Sul in central-western Brazil, where it was collected on the banks of a seasonally dry pond on shallow calcareous soil and limestone

outcrops. Locally abundant or sparse, depending on the season, collected in flower from March to April.

Dimerostemma annuum is the only member in the genus which is a slender annual herb and that has pales slightly conduplicate and not carinate-alate. The distinctiveness of *D. annuum* is supported with nuclear DNA sequences (Moraes et al., submitted), appearing as basal in the molecular analysis. This species shares with *D. humboldtianum* and *D. myrtifolium* similar vestiture of very small, appressed and sparse trichomes. It is distinguished from both in linear to very narrowly oblong-elliptic blades.

Additional specimens examined: BRAZIL. **Mato Grosso do Sul:** Bonito, Fazenda Formoso, Lagoa de Pedras, $21^0$20'S, $56^0$37'W, 3 Apr 2001, *Moraes et al. 629* (TEX, UEC); 23 Apr 2000, *Pott et al. 4554* (CPAP, R, UEC).

Dimerostemma apense (Chodat) M. D. Moraes, Bot. J. Linn. Soc. "submitted". *Aspilia apensis* Chodat, Bull. Herb. Boissier 2 (3): 721. 1903. *Zexmenia apensis* (Chodat) Hassl., Repert. Spec. Nov. Regni Veg. 14: 177. 1915. *Angelphytum apense* (Chodat) Pruski, Compositae Newslett. 34: 2. 1999. SYNTYPES: PARAGUAY: ad marginem silvarum in regione cursus superioris fluminis Apa, Nov, *E. Hassler 7731* (C-n.v., F, G-n.v., NY, photo-G at RB and TEX); in silva pr. Valenzuela, Feb, *E. Hassler 7096* (probable G-n.v.). Lectotypification is deferred until both syntype collections are examined. (Fig. 1 O, Fig. 2 H, Fig. 3 B)

Coarse, robust, *subshrubs* 1-2.5 m high, with short lived aerial stems from a woody caudex. *Leaves* opposite; petioles 0.5-2 cm long; *blades* 8-12(-15) x 3-6(-7.5) cm, membranous, ovate or sometimes narrowly ovate, shortly attenuate, sometimes slightly oblique at base, acuminate at apex, margins serrulate or sometimes serrate, adaxial surface sparsely scabridulous with scattered larger trichomes, the abaxial paler, strigillose, with larger trichomes along the veins. *Phyllaries* the outer 10-30 x 2.5-8 mm, much longer than the inner, oblong to narrowly oblong or oblong-elliptic and slightly constricted and

indurate at base, the inner 5-10 x 2-4 mm, oblong-elliptic, constricted and indurate at base. *Pales* 9-10 x ca. 1.5 mm when folded, with rigid, linear and pungent tip up to 3.5 mm long. *Ray florets* fertile, tube 1-2 mm long, lamina 17-32 x 4-8 mm, oblanceolate to elliptic, slightly setulose abaxially. *Disc florets* with corolla 4-5.5 mm long, lobes abaxially moderately setulose. *Cypselas* 3-6 x 1.2-1.5 mm, wings up to 2 mm wide, the peripheral thickened, trigonous, with much reduced wings to wingless or sometimes with well developed wings on much smaller bodies, densely tuberculate with maturity, the inner flatter, less tuberculate; *pappus* with awns reduced to tooth like projections or sometimes up to 3 mm long, then of one half of the cypsela body length or less, the peripheral mostly awnless, crown 0.2-1 mm high, almost totally fused to the body (more than 2/3), lacerate to fimbriolate.

Distribution, habitat and phenology: Mato Grosso do Sul and neighboring Paraguay, in secondary, gallery, deciduous or semi-deciduous forest, mostly found on shallow calcareous soils at 200-400 m, scattered or sometimes in large population. Collected in flower from November to April.

D. apense is very similar to *D. herzogii* (Hassl.) Pruski from Bolivia in shape of leaves and cypselas, but differs in margins of leaves mostly serrulate (vs. serrate), pales with rigid, acute linear tip up to 3.5 mm long (vs. pales with subulate tip up to 2.5 mm long) and awns that are mostly reduced to tooth like projection (vs. awns well developed, mostly up to 3 mm long). *Dimerostemma apense* (Fig. 1 O) resembles *D. goyazense* (Fig. 1 Q) and *D. bahiense* (Fig. 1 P) in shape of leaves, but is distinguished from all mainly by pales with rigid, acute linear tip up to 3.5 mm long.

Additional specimens examined: BRAZIL. **Mato Grosso do Sul:** Antonio João, Campestre, 16 Mar 1985, *Hatschbach & Zelma 49104* (Z); Bonito, Fazenda Formoso, near the spring of Rio Formoso, $21^0$15'S, $56^0$38'W, 3 Apr 2001, *Moraes et al. 631* (UEC); Corumbá, 2 Apr 1903 *Malme 3016* (R); Corumbá, rd. to Chácara São Marcos, between bairro Cristo Redentor and Cravo

Vermelho, 19^{0}2'S, 57^{0}38'W, 29 Nov 2000, *Moraes & Damasceno 557* (UEC); Corumbá, rd. Monjolo to Lampião Aceso, 19^{0}13'S, 57^{0}29'W, 290 m, *Moraes et al. 615* (TEX, UEC); in front of Morro São Domingos, 19^{0}16'S, 57^{0}38'W, 200 m, 17 Feb 1995, *Pott 2511* (CPAP, UEC); Ladário, Fazenda São Marcelo, Morro Sta. Cruz, 19^{0}10'S, 57^{0}35'W, 400 m, 30 Jan 2001, *Damasceno et al. 2148* (COR, UEC);

PARAGUAY: **Amambay:** Sierra de Amambay, 1907-1908, *Hassler 9969* (F).

Dimerostemma arnottii (Baker) M. D. Moraes, Bot. J. Linn. Soc. "submitted". *Verbesina arnottii* Baker in Martius, Fl. Bras. 6.(3): 215. 1884. *Zexmenia arnottii* (Baker) Hassl., Repert. Spec. Nov. Regni Veg. 14: 264. 1916. *Angelphytum arnottii* (Baker) H. Rob., Proc. Biol. Soc. Wash. 97 (4): 965. 1984. TYPE: PARAGUAY. In campis ad Assomption (protologue), Jan 1873 (label), *Gilbert 1043* (LECTOTYPE here selected: K-n.v., photo-K at UEC). (Fig. 1 F-H, Fig. 2 L, Fig. 3 D)

Verbesina paraguariensis Chodat, Bull. Herb. Boissier sér 2 (3): 722. 1903. SYNTYPES: PARAGUAY: In arenosis pr. Tobaty, Sept 1900, *Hassler 6247* (probable G-n.v.); in campo rupestre in colle Santo Tomas pr. Paraguary, Dec 1900, *Hassler 6482* (probable G-n.v.); in campo pr. Valenzuela, Jan 1900 *Hassler 7017* (BM, K-n.v., photos: F, MO, photo-K at UEC, probable G-n.v.). Lectotypification is deferred until all syntype collections are examined.

Verbesina arnottii Baker var. *angustifolia* Hassl. & Chodat, Bull. Herb. Boissier ser 2 (3): 723. 1903. TYPE: PARAGUAY: pr. Chololo, Jan 1900, *Hassler 6896* (LECTOTYPE here selected: BM; ISOLECTOTYPE: K-n.v, photo-K at UEC).

Verbesina arnottii Baker var. *angustifolia* Hassl. & Chodat, f. *scabriuscula* Hassl. & Chodat, Bull. Herb. Boissier ser 2 (3): 723. 1903. TYPE: PARAGUAY: Cordillera de Altos, Aug, *Hassler 339* (HOLOTYPE: probable in G-n.v.; ISOTYPE: K-n.v., photo-K at UEC).

Verbesina arnottii Baker var. *oblongifolia* Hassl. & Chodat, Bull. Herb. Boissier 2 (3): 723. 1903. TYPE: PARAGUAY: pr. Itacurubi, Sept, *Hassler 1081* (HOLOTYPE: probable in G-n.v.; ISOTYPES: BM, K-n.v., photo-K at UEC).

Verbesina arnottii Baker var. *oblongifolia* Hassl. & Chodat, f. *gracilis* Hassl. & Chodat, Bull. Herb. Boissier 2 (3): 723. 1903. TYPE: PARAGUAY: pr. Caraguatay, Oct, *Hassler 3297* (HOLOTYPE: probable in G-n.v.; ISOTYPES: BM, K-n.v., photo-K at UEC).

Verbesina arnottii Baker var. *tomentosa* Hassl. & Chodat, Bull. Herb. Boissier 2 (3): 723. 1903. TYPE: PARAGUAY: pr. Piribebuy, Dec, *Hassler 6591* (HOLOTYPE: probable in G-n.v.; ISOTYPES: BM, F, K-n.v., S, photo-K at UEC).

Zexmenia arnottii (Baker) Hassl. var. *interea* Hassl. f. *angustifolia* Hassl., Repert. Spec. Nov. Regni Veg. 14: 266. 1916. SYNTYPES: PARAGUAY: Villa Rica, Jan 1905, *Hassler 8578* (BM, F, probable in G-n.v.); Caaguazu, Mar 1905, *Hassler 9154* (BM, F, probable in G-n.v.); locality not indicated, *Hassler 6885a* (probable in G-n.v.); locality not indicated, *Hassler 6247* (probable in G-n.v.). ARGENTINA: Entre Rios, *Lorentz 1441* (probable in B-n.v.). Lectotypification is deferred until all syntype collections are examined.

Zexmenia arnottii (Baker) Hassl. var. *interea* Hassl. f. *angustifolia* Hassl. subf. *gracilis*, Repert. Spec. Nov. Regni Veg. 14: 266. 1916. TYPE: PARAGUAY: Caaguazu, Mar 1905, *Hassler 9211* (HOLOTYPE: probable in G-n.v.; ISOTYPES: BM, F, S).

Zexmenia arnottii (Baker) Hassl. var. *mollis* Hassl. f. *sericea* Hassl., Repert. Spec. Nov. Regni Veg. 14: 267. 1916. SYNTYPES: PARAGUAY: Villa Rica, Jan 1905, *Hassler 8582* (BM, F, probable in G-n.v.); Villa Rica, *Hassler 8582b* (probable in G-n.v.). Lectotypification is deferred until both syntype collections are examined.

Zexmenia arnottii (Baker) Hassl. var. *mollis* Hassl. f. *calvescus* Hassl., Repert. Spec. Nov. Regni Veg. 14: 267. 1916. TYPE: PARAGUAY: Villa Rica, Jan 1905, *Hassler 8582a* (HOLOTYPE: probable in G-n.v.; ISOTYPES: BM, F).

Zexmenia arnottii (Baker) Hassl. var. *myrtifolia* Hassl. f. *intermedia* Hassl., Repert. Spec. Nov. Regni Veg. 14: 268. 1916. TYPE: PARAGUAY: Caaguazu, in regione fluminis Yhú, 1905, *Hassler 9502* (HOLOTYPE: probable in G-n.v.; ISOTYPES: BM, F).

Zexmenia arnottii (Baker) Hassl. var. *viguieroides* (Baker) Hassl. f. *macrocephala* Hassl., Repert. Spec. Nov. Regni Veg. 14: 269. 1916. SYNTYPES: PARAGUAY. Unknown locality, *Hassler 339* (probable in G-n.v.); l.c. *Hassler 6482* (probable in G-n.v.); l.c. *Hassler 7098* (probable in

G-n.v.); Cordillera de Altos, 1897, *Hassler 2081* (BM); in regione lacus Ypacaray, Dec 1913, *Hassler 12417* (BM, C, probable in G-n.v., S, Z);. Lectotypification is deferred until all syntype collections are examined.

Zexmenia arnottii (Baker) Hassl. var. *viguieroides* (Baker) Hassl. f. *guaranitica* Hassl., Repert. Spec. Nov. Regni Veg. 14: 269. 1916. SYNTYPES: PARAGUAY. Unknown locality, *Hassler 339* (probable in G-n.v.); l.c. *Hassler 6482* (probable in G-n.v.); l.c. *Hassler 7098* (probable in G-n.v.); Cordillera de Altos, 1897, *Hassler 2081* (BM); in regione lacus Ypacaray, Dec 1913, *Hassler 12417* (BM, C, probable in G-n.v., S, Z);. Lectotypification is deferred until all syntype collections are examined.

Zexmenia arnottii (Baker) Hassl. var. *virgata* Hassl. f. *graminifolia* Hassl., Repert. Spec. Nov. Regni Veg. 14: 270. 1916. TYPE: PARAGUAY: Sierra de Maracayú, 1898-99, *Hassler 5765* (HOLOTYPE: probable in G-n.v.; ISOTYPE: BM).

Zexmenia oppositifolia A. A. Sáenz, Hickenia 1(54): 285. 1982. *Angelphytum oppositifolium* (A. A. Sáenz) H. Rob., Proc. Biol. Soc. Wash. 97 (4): 968. 1984. *Dimerostemma oppositifolia* (A. A. Sáenz) M. D. Moraes, Bot. J. Linn. Soc. “submitted”. TYPE: ARGENTINA. Prov. Misiones: Depto Apóstoles, San José, Escuela Agrotécnica Pascual Gentilini, Cerro Ceferino, 10 Feb 1978, *A. L. Cabrera et A. A. Sáenz 29129* (HOLOTYPE: SI-n.v.).

Basally woody *perennial herbs* or *subshrubs* up to 1 m high, mostly cespitose, from a xylopodium. *Leaves* mostly alternate, opposite at the base, sometimes a few shoots or all of them may become opposite leaved throughout; *petioles* up to 4 mm long or subsessile; *blades* 3-7(-9) x 0.5-3 cm, submembranous, ovate to lanceolate, sometimes elliptic to obovate or narrowly lanceolate to rarely linear, very shortly attenuate to cuneate at base, acuminate to acute or sometimes obtuse and mucronulate at apex, margins sparsely and obscurely serrulate to serrate, strigillose to velutinous to densely sericeous on both surfaces, abaxially paler, 3-nerved from near to well above the base, subpinnately netted distally or sometimes throughout. *Pyllaries* the outer 8-20(-30) x (1.5-)2-8 mm, oblong to narrowly oblong, slightly constricted and indurate at base or elliptic beyond a short, narrow

oblong base, rarely linear, the inner 8-11 x 2-2.5 mm, narrowly oblong to oblong, indurate at base, constricted and foliaceous at apex to completely scarious. *Pales* 9-11 x ca. 1 mm when folded, obtuse and mucronulate to shortly acuminate or sometimes subulate at the tips. *Ray florets* fertile, tube 2-4 mm long, lamina 11-23 x 3-7 mm, oblong to elliptic to oblanceolate, abaxially glabrous or with a few trichomes. *Disc florets* with corolla 4-5 mm long, lobes abaxially glabrous or with a few trichomes. *Cypselas* 3.5-5.5 x 1.5-2 mm, smooth to finely and sparsely tuberculate, the peripheral trigonous, 3-winged, 3-awned, the inner laterally flattened, the wings 1-2 mm wide, obscurely ciliate especially on the opposite side of pale; *pappus* with awns 1.5-5 mm long, mostly subequal, the longest shorter but not less than ¾ of the cypsela body length, broad to very broad at base, crown 0.5-1 mm high, very fragile, easily bronken, partially fused to the cypsela body (mostly less than 1/3), with lacerate or entire margins.

Distribution, habitat and phenology: The most widespread species in the genus, ranging between the coordinates 22^0-30^0S and 49^0-57^0W, from 94 to ca. 1000 m, in west-central and southern Brazil, adjacent Paraguay and eastern Argentina, with only one collection in Uruguay. In Brazil, it is reported from Mato Grosso do Sul south through São Paulo to Rio Grande do Sul, being abundant in Paraná and apparently local in the State of São Paulo and Santa Catarina. *D. arnottii* is found in open areas of semi-deciduous forest, cerrado, campo, roadside among ruderals and sometimes in swampy areas, mostly on sandy soils. Collected in flower from October to June.

Dimerostemma arnotti is the most polymorphic species in the genus, including considerable leaf variation related to arrangement, size, shape (Fig. 1 F-H) and density of indument. The extremes can be very different, but there are no discontinuities that would allow the practical recognition of varieties or species, and frequently, these variation occur in the same locality. Sáenz (1982) differentiated *Zexmenia oppositifolia* from *Z. arnottii* mainly by its opposite, linear to linear-oblong leaves, which makes us reluctant to accept

taxonomically any forms based on these characteristics. Although we have not examined the type collection of *Zexmenia oppositifolia*, we examined two specimens (*Romanczyk 350*, CTES and *Krapovickas et al. 18252*, CTES), which were cited in the protologue (Sáenz 1982) and agreed with the type illustration.

Dimerostemma arnottii (Fig. 3 D) resembles *D. reitzii* (Fig. 3 E) in shape of cypselas and some specimens of *D. arnottii* with short and narrow leaves (Fig. 1 F) are very similar to *D. reitzii* (Fig. 1 S), but differs in blades never shorter than 3 cm, that are 3-nerved, subpinnately netted distally or throughout (vs. one-nerved blades up to 2.7 cm long).

Dimerostemma arnottii differs further in pappus with mostly subequal awns, which are shorter than the cypsela body (Fig. 3 D), whereas *D. reitzii* has awns mostly unequal, the longest ca. of the same length of the cypsela body or longer (Fig. 3 E). The close relationship between *D. arnottii* and *D. reitzii* is also supported with nuclear DNA sequences (Moraes et al., submitted). *Dimerostemma arnottii* is also similar to *D. myrtifolium* in the overal shape of cypsela. See further commentaries under *D. myrtifolium.*

Additional specimens examined: BRAZIL. **Mato Grosso do Sul:** Amambai, vicinity of tribe Caiuá, 1979, *Garcia 14333* (UEC); 17.6 km from Amambai to Coronel Sapucaia, $23^0$11'S, $55^0$20'W, 27 Mar 2001, *Moraes et al. 618* (UEC); Coronel Sapucaia, corredor internacional, $23^0$19'S, $55^0$33'W, 27 Mar 2001, *Moraes et al. 620* (UEC); 85 km from Campo Grande to Aquidauana, 28 Jan 1979, *Krapovickas & Cristóbal 34431* (CTES); Ribas do Rio Pardo, rio Botas, 25 Jan 1979, *Krapovickas & Cristóbal 34360* (CTES); Rio Brilhante, Casa Branca, 15 Feb 1970, *Hatschbach 23607* (RB); 18 km W of Tucuru, rodovia MS-295, Fazenda Santa Paula, 8 Feb 1993, *Hatschbach et al. 58697* (Z). **Paraná:** Capão Grande, 21 Jan 1909, *Dusén 9054* (S); Desvio Ribas, 20 Jan 1909, *Dusén 7610* (S); Guarapuava, Rio Coutinho,7 Jan 1987, *Cordeiro & Hatschbach 400* (C, S, Z); Jaguariaíva, 5 Feb 1910, *Dusén 9188* (S); 740 m, 19 Nov 1914, *Dusén 16008* (NY, S); *Dusén 16008b* (S); 29 Dec 1914, *Dusén 16205* (S); 18 Dec 1915, *Dusén 17443a* (S); Lageado 5 reis, 18 Nov 1975, *Hatschbach 37086* (NY, RB); 11 km from Jaguariaíva to Itararé, 16 Mar 2000, *Moraes 441* (UEC); road to Arapoti, near boundary, ca. $24^0$8'S, $49^0$20'W, 850-1000 m, 17 Jan 1965, *Smith*

et al. 14701 (F); Lagoa Dourada, 13 Jan 1964, *Pereira & Pabst 8246* (NY); Palmeira, Rodovia BR-277, near Rio Capivara, 27 Dec 1984, *Hatschbach 48821* (C, MO, Z); Ortigueira, Córrego do Leão, 21 Dec 1984, Silva & Hatschbach 269 (HRB); 26 km from Piraí do Sul to Jaguariaíva, 15 Mar 2000, *Moraes 436* (UEC); Ponta Grossa, 11 Dec 1903, *Dusén 2619* (R); 13 Dec 1903, *Dusén 2642* (R); 15 Dec 1903, *Dusén 2730* (R); 17 Nov 1909, *Dusén 7558* (S); 10 Jan 1915, *Dusén 16292* (F, S); above Rio Tibagi at Rodovia do Café, ca. 25^{0}18'S, 50^{0}W, 900 m, 21 Jan 1965, *Smith & Klein 14917* (F); Furnas, 15 Nov 1971, *Santos et al. 3018* (R); Terrinha, 27 Feb 1909, *Dusén 8609* (S); Tibagi, Fazenda Monte Alegre, 22 Feb 1953, *Hatschbach 2982* (SP). **Santa Catarina:** Campos dos Curitibanos, Mar 1877, *Muller 59* (R). **São Paulo:** Itapeva, along the road, 9 Feb 1976, *Gibbs et al. 1631* (UEC); from 43 km of Jaguariaíva to Itararé, 16 Mar 2000, *Moraes 444* (UEC); Rancharia, Rodovia Raposo Tavares, km 516.5, 22^{0}24'S, 51^{0}2'W, 430 m, 14 Feb 1996, *V. C. Souza & J. P. Souza 10900* (UEC). **Rio Grande do Sul:** Arroio dos Ratos to Cachoeira do Sul, km 159, 94 m, 21 Jan 2003, *Magenta & Mondin 501* (UEC); 5 km S of Palmeira das Missões, 13 Dec 1960, *Lindeman & Haas 3637* (UB); Passo do Socorro para Vacarias, 26 Dec 1951, *B. Rambo 51536* (B); 50 km S of Rosario do Sul, 7 Dec 1978, *Krapovickas & Cristóbal 38508* (CTES); ca. 8 km SW of Torres, 10 Feb 1983, *Krapovickas & Cristóbal 38508* (CTES).

PARAGUAY. **Alto Paraná:** 8 km from Hernandarias to Pto. Presidente Stroessner, 7 Dec 1982, *Dlouhy & Casas 7342* (MO); 20 km N of Hernandarias, 10 Jan 1974, *Schinini 8068* (CTES); Rva. Tatí Yupí, 27 Dec 1978, *Itaipú Binacional 93* (MO, CTES); *Itaipú Binacional 100* (MO, CTES). **Caaguazu:** Arroyo Cambay, 32 Km S of Arroyo Yhú, 25^{0}25'S, 55^{0}55'W, 1 Dec 1990, *Zardini & Velázquez 24734* (MO); 2 km N of Arroyo Guaranungua, 25^{0}22'S, 55^{0}55'W, 5 Jan 1991, *Zardini & Velázquez 25662* (MO); edge of Arroyo Taruma, 25^{0}11'S, 55^{0}55'W, 5 Jan 1991, *Zardini & Velázquez 25497*(MO, TEX); 5 km N of Arroyo Guaranunga, 25^{0}19'S, 55^{0}55'W, 12 Jan 1991, *Zardini & Velázquez 25956* (MO); 2 km N of Arroyo Yuquyry, 25^{0}15'S, 55^{0}55'W, 5 Jan 1991, *Zardini & Velázquez 25559* (MO, TEX); vicinity of Caaguazú, Mar 1905, *Hassler 9002* (F); 34 km W of Caaguazú, 8 May 1974, *Schinini 9156* (CTES); 14 km N of Caaguazú, 25^{0}25'S, 56^{0}W, 250m, *Schinini 28092* (CTES); 15 km N of Caaguazú, 8 Feb 1982, *Schinini et al. 21986* (CTES). **Caazapa:** Tavai, 26^{0}10'S, 55^{0}17'W, 21 Dec 1988, *Soria 3046* (MO). **Canendiyú:** 40 Km S of Catueté, 17 Dec

1982, 350 m, *Fdez. Casas 7654* (NY); Katueté, 24^{0}10'S, 54^{0}40'W, 15 Feb 1984, *Hahn 2108a* (MO); Lagunita, 15 Feb 1997, *Marín & Jiménez* 527 (CTES). **Central:** Central and Tororo, 25^{0}15'S, 57^{0}30'W, 13 Jan 1990, *Zardini & Velázquez 18191* (MO); Tarumandy, 2 Apr 1973, *Schinini 6214* (CTES). **Cordillera:** 9 km SE of Emboscada, 25^{0}9'S, 57^{0}14'W, 9 Jun 1990, *Zardini & Velázquez 21092* (MO); Itacuruhí, Dec 1970, *Schinini 3938* (CTES); 3 km from Nueva Colombia, 19 Dec 1987, *Soria* & *Ortiz 1825* (MO); Western side of Rio Piribebuy basin, 25^{0}8'S, 57^{0}18'W, 19 May 1990, *Zardini & Velázquez 20342* (MO); 1 km S of Tobatí, 25^{0}12'S, 57^{0}7'W, 28 May 1988, *Zardini & Velázquez 4302* (MO). **Guairá:** Mbocayaty, 4 Mar 1983, *Bordas 1943* (CTES); 2 Jun 1982, *Bordas 1602* (CTES). **Misiones:** Estancia La soledad, 17 Nov 1956, *Pedersen 4328* (C); 12 km W of San Ignacio, 15 Dec 1978, *Arbo et al. 1827* (F). **Paraguari:** Parque Nacional Ybycui, 26^{0}3'S, 56^{0}50'W, 27 Jan 1989, *Zardini & Velázquez 10364* (MO); 18 Mar 1989, *Zardini & Velázquez 11663* (MO); 21 Dec 1988, *Zardini et al. 9130* (MO). **San Bernardino:** 25^{0}26'S, 56^{0}58'W, 9 Dec 1945, *Teague 635* (BM). **San Pedro:** Alto Paraguay, Primavera, 14 Oct 1955, *Woolston 597* (C, NY, S); 8 km of San Stanislao, 17 Feb 1968, *Krapovickas et al. 13908* (TEX). **Valenzuela:** campo rupestre, Dec 1900, *Hassler 6885a* (BM, **syntype of *V. arnottii* var. *angustifolia***)

ARGENTINA. **Chaco:** 1^0 Mayo, 15 Mar 1961, *Schulz 11547* (F). **Corrientes:** Béron de Astrada, 15 km W of Itá Ibaté, 16 Jan 1977, *Schinini 14079* (CTES, F); Capital, Riachuelo, 15 Feb 1996, *Schinini 30427* (TEX); 7 km E of Corrientes, 27 Nov 1977, *Cristóbal & Krapovickas 1708* (CTES); Concepción; 11 km NW of Santa Rosa, 16 Dec 1977, *Treesens et al. 1000* (CTES); Empedrado, Estancia Las tres Marias, 11 Nov 1962, *Pedersen 6642* (C, TEX, S); General Paz, Los Cubanos, 4 Dec 1944, *Schuwarz 282* (NY, S); Itatí, Ramada Paso, 1 Nov 1970, *Krapovickas & Cristóbal 16482* (C); Ituzaingó, RN 12, 3 km S of A. Itaembé, 27^{0}29'S, 56^{0}4'W, 25 Jan 1976, *Romanczuk 350* (CTES); Isla Apipé Grande, Puerto Mora, 11 Dec 1973, *Krapovickas et al. 24412* (R); RN 12, 17 km E, to San Carlos, 14 Feb 1971, *Krapovickas et al. 18252* (CTES); RN 12, 9 km to San Carlos, 11 Apr 1974, *Krapovickas et al. 24909* (CTES); Mburucuyá, Manantiales, 2 Nov 1945, *Ibarrola 3696* (R); Estancia Santa Teresa, 11 Dec 1951, *Pedersen 1381* (C); 12 km from Mbrucuyá, 4 Dec 1983, *Cowan 4105* (TEX); San Miguel, 21 km S of Loreto, 7 Mar 1974, *Schinini et al. 8274* (CTES); Estancia Santa Teresa, 17 Nov 1949, *Schwarz 8776* (C); Villa Olivari, 24 Nov 1993, *Arbo et al.*

6052 (CTES). **Entre Rios:** in pascuis siccis, s.d., *Tweedie s.n.* (photo-K at UEC, **syntype of *V. arnottii***); **Missiones:** Capital, Arroyo Zaimán, 25 Nov 1994, *Dematteis et al. 345* (CTES); Manuel Belgrano, 4 km S of Bernardo de Irigoyen, 17 Feb 1970, *Marunak 118* (CTES); San Ignacio, Mar 1964, *Crovetto 9897* (CTES); 4 km from San Ignacio to Teyu Cuaré, 14 Jan 1976, *Krapovickas & Cristóbal 28740* (F); 5 km from San Ignacio to Teyu Cuaré, 12 Nov 1976, *Quarín 3492* (C). URUGUAY. **Rio Negro:** OFIR, 27 Nov 1919, *Herter 1020* (M, NY, S, Z).

Dimerostemma bahiense (H. Rob.) M. D. Moraes, Bot. J. Linn. Soc. "submitted".

Angelphytum bahiense H. Rob., Proc. Biol. *Soc*. Wash. 97 (4): 966. 1984. TYPE: BRAZIL. Bahia: Espigão Mestre, extensive limestone outcrop 6 km S of Cocos and adjacent pastures, 520 m, 16 Mar 1972, *W. R. Anderson, M. Stieber, J. H. Kirkbride Jr. 37028* (HOLOTYPE: UB-n.v.; ISOTYPES: F, K-n.v., NY, US-n.v., photo-K at UEC and photo-US at F, G, UEC). (Fig. 1 P, Fig. 2 N, Fig. 3 C)

Basally woody *herbs* or *subshrubs* 1-1.5 mm high, from a woody caudex. *Leaves* opposite; petioles up to 2 cm long; *blades* 7.5-11 x 3.5-5.5 cm, submembranous, ovate, obtuse to subtruncate then shortly attenuate at base, acuminate at apex, margins serrulate, adaxial surface scabridulous, the abaxial paler, strigillose, both surfaces with longer trichomes on the veins. *Phyllaries* the outer 13-37 x 5-11 mm, lanceolate to oblong-elliptic, slightly indurate at base, the inner 5-9 x 2.5-4 mm, oblong-elliptic, constricted and indurate at base to oblong-obovate and more scarious. *Pales* 7-8 x ca. 1.5 mm when folded, deltate (ca. 1 x 1 mm) at the tip. *Ray florets* fertile, tube 2 mm long, lamina 18-20 x 7-8 mm, oblong to elliptic, abaxial surface sparsely setulose toward the base. *Disc florets* with corolla 4-5 mm long, lobes abaxially glabrous or with a few trichomes. *Cypselas* 3.5-4.5 x 1.2-1.5 mm, the peripheral thickened, subquadrangular or trigonous with much reduced wings to wingless or asymmetrically winged, with well developed wings on the opposite side of pale, densely tuberculate, the inner laterally flattened, sparsely tuberculate, wings up to 1.2 mm wide; *pappus* with awns mostly reduced to tooth like

projections or sometimes awnless, crown 0.5-0.8 mm high, almost totally fused to the body (mostly more than 2/3), with erose to fimbriolate margins.

Distribution, habitat and phenology: Apparently restricted to Cocos, near 14^0S and 44^0W, at 520-560 m, in southwest Bahia, a region of tall semi-deciduous and deciduos forests. Found growing on sandy soil in partial shade, close to an extensive limestone outcrop, or in shrubby woods on hills of gentle slope. Collected with flowers in March.

Dimerostemma bahiense is morphologically related to *D. goyazense* and *D. apense*, but differs from the first in outer phyllaries larger and pappus characterized by awns mostly reduced to tooth like projection and from the second in having pales deltate at the tip.

Additional specimens examined: BRAZIL. **Bahia:** ca. 13 km S of Cocos, 560 m, 15 Mar 1972, *Anderson et al. 36968* (RB); 6 km S of Cocos, 22 Mar 2000, *Moraes & Aona 447*, *448* (TEX, UEC).

Dimerostemma bishopii H. Rob, Phytologia 49: 275. 1981. TYPE: BRAZIL. Goiás: 68 km NW along road from Iaciara to Nova Roma,1400 ft, 5 Feb 1981, *R. M. King & L. E. Bishop 8803* (HOLOTYPE: UB; ISOTYPES: K-n.v., US-n.v., photo-K at UEC, photo-US at B, F, G, MO, NY, S, UEC). (Fig. 1 D, Fig. 3 Q)

Coarse, robust *subshrubs* up to 1.5 m high, from a xylopodium. *Leaves* opposite; petioles 5-13 mm long; *blades* 5-9 x 3.5-6.5 cm ovate to broadly ovate, rounded to truncate or subcordate at base, very shortly acuminate to acute at apex, margins minutely serrulate, adaxial surface sparsely pillose, the abaxial paler, more densely pillose to subvelutinous. *Phyllaries* the outer 10-25 x 5-14 mm, elliptic, the inner 6-8 x 3-5 mm, elliptic to obovate or oblong, sometimes constricted at the base. *Pales* 6-7 x ca. 1 mm when folded, with obtuse to acute tip up to 1 mm long. *Ray florets* sterile, tube 0.5-1 mm long, lamina 15-17 x 5-7 mm, elliptic to oblong or obovate, sparsely setullose abaxially. *Disc florets* with corollas 3.5-4.5 mm long, lobes glabrous or with a few trichomes abaxially. *Cypselas* ca. 3 x 1.3 mm, thickened, subquadrangular, tuberculate at maturity,

wingless or wings much reduced to a narrow margin; *pappus* awnless or sometimes with awns much reduced to tooth like projections ca. 0.2 mm long, crown reduced to a minutely erose margin.

Distribution, habitat and phenology: Endemic to Goiás, found growing on calcareous soils in partial shade under cerrado to deciduous forest transition at ca. 420 to 570 m. Collected with flowers from February to March, with old heads in April.

Dimerostemma bishopii resembles *D. virgosum* and *D. species nova* in thickened, subquadrangular, tuberculate cypselas, that are wingless or with wings much reduced and especially in having pappus mostly awnless (Fig. 3 Q - S). It differs from both primarily in leaf blades that are rounded to truncate or subcordate at the base.

Additional specimens examined: BRAZIL. **Goiás:** Nova Roma, ca. 1.5 km to ferryboat, 10 Apr 2001, *Moraes & Alvarenga 640* (TEX, UEC); Fazenda Sítio Novo, to ferryboat on Rio Paraná, $13^0$43'S, $46^0$52'W, 565 m, 1 Mar 2000, *Silva & Alvarenga 4309* (IBGE).

Dimerostemma brasilianum Cass., Bull. Sci. Soc. Philom. Paris, 58: 1818, as *Dimerostemma brasiliana*. TYPE: herbiers de Jussieu et Desfontaines, sur des échantillons aportés de Lisbonne par Geoffrey, et originaires du Brésil (HOLOTYPE: P–n.v., photos: F, RB). (Fig. 1 C, Fig. 2 C, Fig. 3 I)

Serpaea ovata Gardner, London J. Bot. 7: 296. 1848. *Oyedaea ovata* (Gardner) Baker in Martius, Fl. Bras. 6(3) 1884. TYPE: BRAZIL. Goyaz: dry upland campos near Arrayas, Apr 1840, *Gardner 3852* (HOLOTYPE: K-n.v., photo-K at UEC; ISOTYPES: BM, G, K-n.v., NY, photos: F, MO, RB, photo-K at UEC).

Oyedaea rotundifolia Sch. Bip. ex Baker in Martius, Fl. Bras. 6 (3): 208. 1884. *Dimerostemma rotundifolium* (Baker) S.F. Blake, Contr. Gray. Herb. n.s. 52: 13. 1917. TYPE: BRAZIL. São Paulo: near São Carlos, *Riedel 1852* (LECTOTYPE selected by Blake, 1917: G-n.v., K-n.v., photo-K at UEC; probable ISOLECTOTYPES: F, K-n.v., P-n.v., RB, photo-K at UEC).

Basally woody *perennial herbs* or *subshrubs* 0,5-1 m high, cespitose from a xylopodium. *Leaves* opposite throughout or sometimes alternate distally on the peduncles; petioles up to 7 mm long; *blades* 3-5 x 2.2-5.5 cm, subchartaceous, broadly ovate to orbicular, rounded to truncate to subcordate at base, rounded to obtuse at apex, margins crenate-serrulate or sometimes serrulate, adaxial surface subtomentose or sometimes pilose-strigillose, mostly soft to the touch, the abaxial tomentose, grayish, 3-nerved from near to well above the base, mostly reticulate. *Peduncles* mostly slender or somewhat stout; *heads* subglobose; *phyllaries* the outer 7-13 x 5-10 mm, broadly ovate to elliptic, the inner 6-10 x 3-5 mm, elliptic, constricted at base to obovate. *Pales* 9-11 x ca. 2 mm when folded, with triangular to subulate tip 1-1.5 mm long. *Ray florets* absent or heads with a few small rays in transition to a tubulate shapeless than 10 mm long, rarely with deeply cleft linear laminas. *Disc florets* with corollas 4.5-6 mm long, lobes with a few trichomes abaxially. *Cypselas* 3.5-4.5 x 1.2-2 mm, slightly flattened, smooth or rarely sparsely and finely tuberculate, wings 0.5-1.2 mm wide, ciliate on the margin opposite the pale; *pappus* with awns 3-5.5 mm long, ca. the same length, longer or not less than ¾ of the cypsela body, very broad and sometimes decurrent at base, crown up to ca. 1.5 mm high, mostly laterally parted with squamelloid processes between the awns.

Distribution, habitat and phenology: Brazil – relatively abundant in Minas Gerais and Goiás, apparently local in Distrito Federal, Mato Grosso do Sul and São Paulo. It occurs in cerrado, campo and campo rupestre, between the coordinates 14^0-21^0S and 43^0-50^0W, at 900-1700 m, in flower from January to April.

Morphological comparisons have revealed that *D. rotundifolium* is synonymous with *D. brasilianum*. The placement of *D. lippioides* under the synonymy of *D. brasilianum* by Robinson (1984) is not accepted here. *Dimerostemma brasilianum* differs from *D. lippioides* in blades mostly subtomentose, soft to the touch, 3-nerved from near to well above the base - Fig. 1 C (vs. hispidulous, mostly asperous to the touch, always 3-nerved

from the base - Fig. 1 B); peduncles mostly slender (vs. stout, mostly elongated and leafless); involucres subglobose – Fig. 2C (vs. broadly campanulate – Fig. 2B); ray florets mostly absent or in transition to tubulate (vs. well developed laminas); cypselas with much longer awns and crown with squamelloid processes between the awns – Fig. 3 I (vs. without or sometimes with lateral squamelloid processes – Fig. 3 J).

Additional specimens examined: BRAZIL. **Distrito Federal:** Brasília, Bacía do Rio Bartolomeu, on Road DF 15, 9 Mar 1981, *Heringer et al. 6369* (IBGE). **Goiás:** 8 km N of Alto Paraíso de Goiás, Chapada dos Veadeiros, 1500 m, 6 Mar 1973, *Anderson 6438* (NY, UB); 12 S of Alto of Alto Paraíso de Goiás, Chapada dos Veadeiros, 3400 ft, 8 Febr 1981, *King & Bishop 8865* (UB); ca. 26 Km N of Alto Paraíso de Goiás, 12 Apr 2001, *Moraes 649* (UEC); ca. 10 Km S of Alto Paraíso de Goiás, $14^0$14'S, $47^0$29'W, ca. 1200 m, 1 Mar 1999, *Moraes 395* (UEC); ca. 11 Km S of Alto Paraíso de Goiás, 5 Mar 1999, *Moraes 405* (UEC); ca. 8 km from São Jorge to Alto Paraíso de Goiás, $14^0$9'S, $49^0$46'W, ca. 1200 m, 1 Mar 1999, *Moraes 393, 394* (UEC); São Jorge to Vale da Lua, 28 Feb 1999, *Moraes et al. 391* (UEC); 5 Mar 1999, *Moraes 403* (UEC); ca. 35 km NE of Catalão, 900 m, 24 Jan 1970, *Irwin et al. 25266* (BM, NY, UB); Chapadão do Céu, Parque Nacional das Emas, 5 Apr 1999, *Batalha 3161* (UEC); 20 km N of Corumbá de Goiás, ca. 1150 m, 18 Jan 1968, *Irwin et al. 18790* (F, G, NY, UB); Cristalina to Cachoeira do Arrojado, 1200 m, 24 Jan 1988, *Hatschbach & Cordeiro 51816* (C, NY, S); Cristalina to Salto do Arrojado, 22 Jan 1997, *Hatschbach et al. 66132* (BHCBC, NY, S); Cristalina, 2 Feb 1967, *Heringer 11336* (UB); ca. 2 km N of Cristalina, 1250 m, 2 Mar 1966, *Irwin et al. 13294* (NY); 20 km N of Cristalina, 2200 ft, 13 Feb 1981, *king & Bishop 8946* (UB); ca. 2 km N of Cristalina, 6 Mar 1999, *Moraes 408* (UEC); vicinity of Portelandia, 15 Feb 1974, *Hatshbach 34239* (Z); Silvânia, $16^0$42'S, $48^0$36'W, 12 Jan 1989, *Filgueiras et al. 1793* (IBGE). **Minas Gerais:** Araxá, 5 Feb 1956, *Macedo 4258* (RB); Barreiro, 10 Feb 1951, *Macedo 3138* (RB); 45 km SE of Belo Horizonte, ca. 1500 m, 9 Feb 1968, *Irwin et al. 19703* (F, NY, UB); 44 km of Belo Horizonte, 1300 m, 16 Mar 1957, *Pereira & Pabst 3252* (F); Parque da Manguabeiras, 26 Jan 1996, *Silveira 31* (BHCB); Caxambú to Pouso Alto, 29 Mar 1964, *Trinta & Fromm 684* (M, R); Congonhas do Campo 16 Mar 1957, *Pereira & Pabst 3209* (F); 13 km E of Diamantina, 1000m, 14 Mar 1970, *Irwin et al. 27510* (F, NY, UB); 10 km S of Diamantina, 18 Jan 1981, *King & Bishop 8541* (UB);

Diamantina, 3 Apr 1957, *Pereira & Pabst 3671* (F); 31 km NE of Francisco de Sá, 1100 m, 11 Feb 1969, *Irwin et al. 23067* (NY, UB); 36 km NE of Francisco de Sá, 1100 m, 12 Feb 1969, *Irwin et al. 23178* (NY, UB); 8 km N of Gouveia, 1220 m, 3 Feb 1972, *Anderson et al. 35273* (NY); 2 km from Ibiá on BR 262, $19^0$34'S, $46^0$29'W, 2 Mar 1989, *Walter et al. 56* (IBGE, UB); Pico do Itabirito, 24 Mar 1994, *Teixeira s.n.* (BHCB-24988); Ituitaba, 19 Jan 1956, *Macedo 4194* (RB); ca. 25 km NE of Patrocínio, 1050 m, 28 Jan 1970, *Irwin et al. 25502* (C, F, NY, SP, UB); Santa Rita de Cassia, Morro de Furna, Mar 1945, *Vidal 529* (R); 7-12 km N of Santana do Riacho, ca. $19^0$10'S, $43^0$41'W, 11 Feb 1991, *Arbo et al. 4828* (CTES, SPF); Serra da Lapinha, 27 Mar 1991, *Pirani et al. CFSC-12198* (UEC); km 106 on road from Belo Horizonte to Conceição do Mato Dentro, 940-1000 m, 16 Feb 1982, *Lewis et al. CFSC-7753* (UEC); 3 km N of São João da Chapada, 1200 m, 28 Mar 1970, *Irwin et al. 28463* (F, NY, UB);Thermópolis, Chapadão do Jacuhy, 1700 m, Apr 1945, *Vidal 862* (R); Uberlândia, Clube de caça e pesca Itororó, 30 Jan 1996, *Lenza & Barbosa 308* (HUFU); Estação Ecologica do Panga, 19 Jan 1993, *Rossi et al. 8* (HUFU); on road from Uberlândia to Patos de Minas, $18^0$53'S, $46^0$54'W, 28 Feb 1989, *Mendonça et al. 1207* (IBGE, UB). **Mato Grosso do Sul:** in campis ad Cuiabá, *Manso 211* (photo-K at UEC, **Syntype of *O. rotundifolia***); vic. Rio Verde, 10 Feb 1974, *Hatschbach 33995* (Z). **São Paulo:** Campos do Jordão, Apr 1937, *Laustyack s.n.* (RB).

Dimerostemma episcopale (H. Rob.) H. Rob., Proc. Biol. Soc. Wash. 97 (3): 623. 1984.

Oyedaea episcopalis H. Rob., Phytologia 49 (3): 276. 1981. TYPE: BRAZIL. Bahia: 14 km NW from the town of Rio das Contas along road to Pico das Almas, 3300 ft., 24 Jan 1981, *R. M. King & L. E. Bishop 8633* (HOLOTYPE: UB; ISOTYPES: MO, K-n.v., UC-n.v., US-n.v., photo-K at UEC, photo-US at B, C, F, G, NY and UEC). (Fig. 1 M, Fig. 2 D, Fig. 3 M)

Coarse, robust *subshrubs* 1.5-2 m high, from a xylopodium. *Leaves* opposite; *petioles* 2-10 mm long; *blades* (2-)2.5-7.5 x 1-3.8 cm, subchartaceous, ovate to elliptic, shortly to very shortly attenuate at base, acute to shortly acuminate at apex, margins serrulate to serrate, the adaxial surface bullate, strigose, the abaxial paler, densely tomentose to villous, sparsely so along the veins, 3-nerved, reticulate and pinnately netted

distally. *Phyllaries* the outer 6-20 x 2-8 mm, mostly much longer than the inner, spreading, elliptic to narrowly oblong or lanceolate, sometimes slightly indurate and constricted at base, obtuse, sometimes acute and mucronulate at apex, the inner 5-7 x 2-3 mm, ovate to slightly obovate, obtuse to acute, mucronulate at apex. *Pales* 7-9 x ca. 1.2 mm when folded, stramineous, rounded to obtuse or sometimes deltate (1:1 l/w) at the tip. *Ray florets* sterile, tube 1-2 mm long, lamina 8-17 x 3-6 mm, mostly yellow, rarely purplish along the veins, elliptic to obovate, mostly with deeply cut lobes, sparsely setulose abaxially. *Disc florets* with corollas 4-5 mm long, sometimes sparsely setulose along the veins and at the abaxial side of lobes. *Cypselas* 4-4.8 x 1.5-2 mm, slightly thickened, subquadrangular, with a tendency for being densely tuberculate, wings 0.5-1 mm wide; *pappus* with awns reduced to tooth like projections or less than one half of the cypsela body length, crown 0.2-0.8 mm high, partially fused (usually less than 1/3) with laciniate to fimbriolate or lacerate margins.

Distribution, habitat and phenology: Endemic to the State of Bahia (near 13^0S, 41^0W), mostly in cerrado-campo rupestre transition at 990-1700 m, on gravelly or sandy soils among large boulders. Collected in flower from November to March, sporadically in September.

In the molecular analysis of *Dimerostemma* (Moraes et al. submitted), *D. episcopale* and *D. grazielae* are resolved as sisters to each other, supporting their close morphological affinity. Both occur in a similar habitat at approximately the same latitude and altitude. *Dimerostemma grazielae*, endemic to Chapada dos Veadeiros in east-central Goiás (near 14^0S, 47^0W), and *D. episcopale*, occurring more at east in the Chapada Diamantina near Rio de Contas, Bahia, are geographically separated by ca. of six degrees of longitude.

These species share similar leaves and cypsela (Fig. 1 M – N and Fig. 2 D - E), consequently *D. grazielae* could be treated as a subspecies of *D. episcopale*, but because

their geographical isolation and the following morphological differences, we consider them two distinct species. *Dimerostemma episcopale* is distinguished in having broader outer phyllaries (Fig. 2 D), not linear or with a long linear base (Fig. 2 E), pales with mostly rounded to obtuse tip, not triangular, rigid, acute tip. *Dimerostemma episcopale* differs further in larger, mostly yellow ray florets with lobes deeply cut (vs. mostly purplish with lobes shallowly cut or entire) and cypselas with a tendency of being densely tuberculate (vs. mostly smooth).

Additional specimens examined: BRAZIL. Bahia: Abaíra, 12 km from Abaíra, on rd. to Catolés, $13^0$11'S, $41^0$49'W, 28 Mar 1985, *Fonseca & Araújo 462* (IBGE); subida da Forquilha da Serra, $13^0$17'S, $41^0$53'W, 1400-1600 m, 23 Dec 1991, *Hind et al. 50292* (MO); near Catolés de Cima, Rio Agua Limpa, 30 Jan 1992, *Hind & Pirani 51335* (MO); Piatã, 8 km from Inubia to Piatã, $13^0$5'S, $41^0$56'W, 1320 m, 11 Nov 1996, *Hind & Bautista 4211* (IBGE); Quebrada da Serra do Atalho, $13^0$13'S, $41^0$50'W, 1600-1700 m, 26 Dec 1991, *Harley et al. H 50387* (MO); Rio de Contas, Mato Grosso, 1350 m, 20 Jan 1984, *Hatschbach 47414* (MO, Z); 17 Set 1989, *Hatschbach & Nicolack 53432* (C, Z); Agua Quente, $13^0$30'S, $41^0$59'W, 1400 m, 30 Nov 1989, Harley et al. 26502 (UEC); ca. 15 km from Rio de Contas to Pico das Almas, ca. 1140m, 23 Mar 2000, *Moraes & Aona 449* (UEC); 12 km from Rio de Contas to Vila de Mato Grosso, 23 Mar 2000, *Moraes & Aona 454* (UEC); subida da Silvínia to Pico das Almas, 24 Mar 2000, *Moraes & Aona 456* (UEC); Pico das Almas, Campo do Queiroz 24 Mar 2000, Moraes & Aona 468 (UEC); trail to Pico do Itobira, 26 Mar 2000, *Moraes & Aona 513* (UEC).

Dimerostemma goyazense (Gardner) M. D. Moraes, Bot. J. Linn. Soc., "submitted".

Lipochaeta goyazensis Gardner, London J. Bot. 7: 406. 1848. *Zexmenia goyazensis* (Gardner) Benth., Gen. Pl. 2: 373. 1873. *Angelphytum goyazense* (Gardner) H. Rob. & W. L. Wagner, Brittonia, 53: 559. 2001. TYPE: BRAZIL. Goiás: near S. Domingos, Mar-May 1840 (protologue), 1841 (label), *Gardner 4235* (LECTOTYPE here selected: K-n.v., photo-K at UEC; ISOLECTOTYPES: K-n.v., photo-K at UEC). (Fig. 1 Q, Fig. 2 F, Fig. 3 O)

Coarse, robust *subshrubs* 1.5-2 m high, from a woody caudex. *Leaves* opposite; *petioles* 1-4.5 cm long; *blades* 8-16 x 3-8.5 cm, submembranous, ovate, obtuse to rounded then shortly or very shortly attenuate at base, acuminate at apex, margins serrulate, adaxial surface sparsely scabridulous, the abaxial sparsely to densely strigillose or subtomentose, both surfaces with larger trichomes on veins. *Phyllaries* the outer 8-20 x 2.5-6 mm, oblong to narrowly oblong or elliptic, slightly indurate at base, the inner 5-8 x 2-5 mm, oblong-obovate, indurate at base and more scarious. *Pales* 7-8 x ca. 1.2 mm when folded, with subulate tip. *Ray florets* fertile, tube 1-1.5 mm, lamina 10.3-25 x 5-6 mm, oblong to elliptic or oblanceolate. *Disc florets* 4.5-6 mm long, lobes sparsely setulose abaxially. *Cypselas* 2.5-4.5 x 1.2-1.5 mm, the peripheral usually trigonous, awnless and wingless, the inner thickened, subquadrangular to slightly flattened, wingless or with wings 0.2-1 mm wide, usually asymetrically winged with wings wider on the opposite side of pale; *pappus* mostly one-awned, with the one awn on the opposite side of pale up to 2 mm long or awnless, crown 0.2-1 mm high, partially fused to the body (less than 1/3) with laciniate to fimbriolate margins.

Distribution, habitat and phenology: This species occurs in the state of Goiás and neighboring Minas Gerais. Found at the margins of tall deciduous forests, at ca. 500 m or higher altitudes, growing in partial shade in pockets of soil among limestone boulders. Collected in flower from February to April, with old heads in June.

Dimerostemma goyazense is similar to *D. bahiense* and *D. apense*, sharing leaves with the same shape and size (Fig. 1 O - Q), but differs from both mainly in pappus mostly one-awned.

Additional specimens examined: BRAZIL. **Goiás:** near Villa de Arrayas, Mar-May, 1840, *Gardner 3847* (photo-K at UEC, **syntype of *L. goyazensis***); Distrito Federal, Brasília, Fercal, 6 Apr 1961, *Heringer 8182* (RB, UB); 24 Jun 1965, *Sucre & Heringer 616* (RB-2, UB); Nova Roma, Fazenda Sta. Clara, $13^0$45'S, $46^0$51'W, 485 m, 29 Feb 2000, *Mendonça et al. 4097* (IBGE); from

Nova Roma to Iaciara, Fazenda Sta. Clara, at the bottom of first hill to the left, 10 Apr 2001, *Moraes & Alvarenga 636* (TEX, UEC). **Minas Gerais:** 15 km W of Januária on rd. to Serra das Araras, 575-650 m, 20 Apr 1973, *Anderson 9218* (RB).

Dimerostemma grazielae H. Rob., Proc. Biol. Soc. Wash. 97 (3): 623. 1984. TYPE: BRAZIL. Goiás: Chapada dos Veadeiros, Cerrado on steep rocky slopes, surrounded by Campo, ca. 19 km N of Alto Paraíso, ca. 1250 m, 20 Mar 1971, *H. S. Irwin, R. M. Harley & G. L. Smith 32779* (HOLOTYPE: UB-n.v.; ISOTYPES: G, K-n.v., NY, US-n.v., photo-K at UEC, photo-US at UEC). (Fig. 1 N, Fig. 2 E, Fig. 3 N)

Coarse, robust *subshrubs* 1-1.7 m high, from a xylopodium. *Leaves* opposite; *petioles* up to 5 mm long; *blades* 2.8-9 x 1-3.5 cm, subchartaceous, ovate or sometimes oblong to elliptic, attenuate at base, acute to shortly acuminate at apex, margins serrate to serrulate, the adaxial surface scabridulous with scattered larger trichomes to densely strigose, sometimes subullate, the abaxial paler, densely strigose to vilous, prominentely reticulate. *Phyllaries* the outer 10-34 x 1.2-1.5 mm, much longer than the inner, spreading mostly linear or elliptic with a long linear base, rarely narrowly oblong, indurate and broader at the very base, acute to very shortly acuminate and mucronulate at apex, the inner 4.5-6 x 2-4 mm, elliptic to obovate to oblong, acute to shortly acuminate or shortly caudate at apex. *Pales* 7-10 x 1-1.5 mm when folded, with mostly purple, triangular, rigid and acute tip. *Ray florets* sterile, tube ca. 1 mm long, lamina 8-10 x 3-4 mm, purplish, yellowish with purple veins or sometimes yellow, elliptic to ovate to oblong, lobes mostly shallowly cut or entire, abaxially glabrous or sparsely setulose toward base. *Disc florets* with corollas 4-5 mm long, sometimes sparsely setulose along the veins and at the abaxial side of lobes. *Cypselas* 3.5-4.8 x 1.5-2 mm, slightly thickened, subquadrangular, with a tendency for being smooth, wings 0.2-0.8 mm wide; *pappus* with awns reduced to tooth like projection or less than one half of the cypsela body length or sometimes awnless, crown 0.2-0.8 mm

high, usually almost completely fused to the body, with fimbriolate to lacerate or laciniate margins.

Distribution, habitat and phenology: D. grazielae has a limited geographical area near Alto Paraíso de Goiás in the Chapada dos Veadeiros, east-central Goiás (near 14^0S, 47^0W). Found in campo rupestre or cerrado-campo rupestre transition at 950-1600 m, on steep rocky slopes or more often on sandy soils among large boulders surrounded by campo, usually in association with *Syagrus* sp., a small palm tree of ca. 1 m tall. Collected in flower from February to April.

Dimerostemma grazielae is very closely related to *D. episcopale*, sharing similar leaves and cypselas (Fig. 1 M – N and Fig. 2 D – E). See further commentaries under *D. episcopale*.

Additional specimens examined: BRAZIL. **Goiás:** 1 km E of Alto Paraíso de Goiás on rd. to Nova Roma, ca. 1300 m, 5 Mar 1973, *Anderson 6346* (UB); 20 km N of Alto Paraíso, 1600 m, 6 Mar 1973, *Anderson 6453* (UB, NY); 5 km E of Alto Paraíso, Chapada dos Veadeiros, 14^0S, 47^0W, 1500 m, 26 Jan 1979, *Gates & Estabrook 65* (NY, UB); ca. 7 km W of Veadeiros, 950 m, 15 Feb 1966, *Irwin et al. 12903* (paratypes at C, MO, NY, S); ca. 42 km N of Alto Paraíso, ca. 1250 m, 25 Mar 1971, *Irwin et al. 33151* (paratype at NY); ca. 42 km from Alto Paraíso to Terezina de Goiás, $13^0$52'S, $47^0$20'W, ca. 1120 m, 2 Mar 1999, *Moraes 398* (UEC); ca. 16 km from Alto Paraíso to Terezina de Goiás, 12 Apr 2001, *Moraes 647* (TEX, UEC); 5-12 km S of Alto Paraíso, 3300-3800 feet, 8 Feb 1981, *King & Bishop* (UB).

Dimerostemma humboldtianum (Gardner) H. Rob., Proc. Biol. Soc. Wash. 97 (3): 624. 1984. *Viguiera humboldtiana* Gardner, London J. Bot. 7: 398. 1848. *Oyedaea humboldtiana* (Gardner) Baker, in C. Martius, Fl. Bras. 6 (3): 206. 1884. TYPE: BRAZIL. Goyaz: arid upland campos near Nossa Senhora d'Abadia, May 1840, G. Gardner 4239 (HOLOTYPE: BM; ISOTYPES: G, K-n.v., NY, F (photo), photo-K and photo-US at UEC). (Fig. 1 K, Fig. 2 K, Fig. 3 L)

Basally woody *perennial herbs* or *subshrubs* 25-60 cm high, cespitose from a xylopodium; *stems* with vegetative shoots distally at the base of the peduncles. *Leaves* opposite, sometimes alternate distally on the peduncles; *petioles* up to 2 mm long; *blades* 2-4(-5.5) x 1-1.4(-2.5) cm, submembranous, oblong to elliptic, mostly drying conduplicate and thus becoming falcate shaped, shortly cuneate at base, the proximal blades usually obtuse to acute at apex, the distal ones acute to shortly acuminate, margins minutely serrate, both surfaces with trichomes so small appressed and sparse that the blades appear subglabrate, appressed strigillose along the veins, the abaxial veins more densely so, rarely both surfaces pilose (in *H. S. Irwin et al*. 8065, NY). *Heads* solitary at the end of primary shoots; *phyllaries* the outer 10-20 x 2-7 mm, elliptic to narrowly oblong, slightly constricted at the base, the inner 7-12 x 2-3 mm, like the outer but narrower. *Pales* 7-9 x 8-12 mm when folded, with subulate or triangular tip up to ca. 1.5 mm long. *Ray florets* sterile, tube 1.5-1.8 mm long, lamina 17-22 x 4-6 mm, oblanceolate to narrowly oblong, sparsely setulose abaxially, 2-3 lobes irregularly cut or sometimes entire. *Disc florets* with corollas 4-5 mm long, lobes glabrous. *Cypselas* 3.5-5 x ca. 2 mm, moderately flattened, subquadrangular, usually with longitudinal ridges, not tuberculate, wings 0.2-0.8 mm wide; *pappus* with awns 1-2.8 mm long, relatively narrow at base, mostly less than one half the cypsela body length, crown 0.5-1.2 mm high, partially fused to the body (less than 1/3), with laciniate to lacerate margins.

Distribution, habitat and phenology: Restrict to DF, with one collection in Niquelândia, Goiás (ca. 200 km by air from DF). Except for the latter, all the others were gathered in recently burned campo cerrado. Collected with flowers in September-October, earlier than most species in the genus.

Among all especies of *Dimerostemma*, none other than this has vegetative shoots distally on the peduncle and most leaves drying conduplicate, consequently becoming falcate shaped.

Additional specimens examined: BRAZIL. **Distrito Federal:** Brasília, 1964, *Barroso 525* (UB); Universidade de Brasília, 10 Sep 1962, *Heringer 9015* (NY, SP); Chapada da Contagem, ca. 25 km NE of Brasília, 1000 m, 7 Sep 1965, *Irwin et al. 8065* (NY); between Brasília and Sobradinho, 1000 m, 13 Oct 1965 *Irwin et al. 9193* (NY, UB); Brasília, ca. 30 km from trevo Colorado to Lago Oeste, Poço Azul, 28 Oct 2000, *Moraes & Oliveira 540* (TEX, UEC); in front of Zoobotânico, 26 Oct 1965, *Sucre 874* (HB, M). **Goiás:** ca. 8 km from Niquelândia to Cia de Níquel Tocantins, 19 Oct 1996, *Mendonça et al 2872* (IBGE).

Dimerostemma lippioides (Baker) S.F. Blake, Contr. Gray. Herb. n.s. 52: 13. 1917. *Oyedaea lippioides* Baker in Martius, Fl. Bras. 6 (3): 208. 1884. TYPE: BRAZIL. Minas Gerais: near Caldas, *Pohl 571* (LECTOTYPE here selected: K-n.v., photo-K at UEC; ISOTYPE: K-n.v., photo-K at UEC). (Fig. 1 B, Fig. 2 B, Fig. 3 J)

Basally woody *perennial herbs* or *subshrubs* 0,5-1 m high, cespitose from a xylopodium. *Leaves* mostly opposite throughout or sometimes alternate distally; *petioles* up to 7 mm long; *blades* 3-7 x 2.8-6 cm, subchartaceous, broadly elliptic to broadly ovate to orbicular, rounded to truncate at base, rounded to obtuse at apex, margins serrulate or sometimes crenulate-serrulate, both surfaces mostly hispidulous or rarely subtomentose, usually asperous to the touch, the abaxial dull cinereous, more densely indumented, always 3-nerved from the base and prominently reticulate. *Peduncles* stout, mostly elongated and leafless; *heads* campanulate. *Phyllaries* the outer 7-25 x 5-20 mm, elliptic or sometimes ovate, not or only slightly indurate at base, the inner 6-16 x 4-10 mm, elliptic, constricted and indurate at base to oblong and more scarious. *Pales* 8-9.5 x 1.2-2 mm when folded, with triangular tip up to 1 mm long. *Ray florets* sterile lacking style, tube 2-3 mm long, lamina 8-20 x 2.5-4 mm, oblong, sometimes elliptic or obovate, sparsely setulose abaxially. *Disc florets* with corollas 5-6.8 mm long, lobes with a few trichomes abaxially. *Cypselas* 3.5-5 x 1.2-2.2 mm, laterally flattened, mostly with smooth faces

without ridges, broady winged with wings 0.7-1.8 mm wide, ciliate on the margin opposite the pale; *pappus* with awns 1-3 mm long, broad to very broad at base, mostly subequal, the longest awn are mostly ca. one half or less than ¾ of the cypsela body length, crown ca. 0.2(-0,5) mm high, inconspicuous, almost totally fused to the cypsela body, with entire margins, sometimes with squamelloid processes partially fused to the internal side of awn base.

Distribution, habitat and phenology: Restricted to Brazil in Distrito Federal, Goiás and adjacent Minas Gerais, apparently local in Mato Grosso, Bahia and São Paulo. Reported from campo and cerrado on mostly red or sandy clay soils at 850 to 1400 m. Collect in flower from November to May and sporadically in July.

All specimens occurring in Brazil, which were cited by Robinson (1984) as *Dimerostemma asperatum* S. F. Blake, are treated here as *D. lippioides*. We conceive *D. asperatum* restricted to Bolivia, sharing with *D. lippioides* similar leaves, but distinguished in cypselas with wings reduced to a narrow margin (vs. well developed wings), and pappus with a conspicuous crown that is partially fused to the cypsela body (vs. inconspicuous and almost totally fused to the cypsela body).

D. lippioides is vegetatively similar to *D. brasilianum* and *D. vestitum*, sharing with them broadly ovate to orbiculate leaves (Fig. 1 A - C). This affinity is supported with ITS rDNA sequences (Moraes et al. submitted). See also commentaries under *D. brasilianum* and *D. vestitum.*

The typical *D. lippioides* differs from the typical *D. vestitum* in opposite leaves (vs. alternate leaves), blades that are hispidulous (vs. tomentose), always 3-nervate from the base (vs. 3-nervate from near to above the base); flattened broadly winged cypselas, with smooth faces – Fig. 3 J (vs. thickened wingless, with longitudinal ridges - Fig. 3 K); and entire margins between the awns (vs. ciliate margins).

D. lippioides is particularly abundant in Distrito Federal, where it grows sympatrically with *D. vestitum.* Some specimens from this area (e.g. *Heringer 16731* MO, IBGE and *Moraes 572*, *581* UEC) have opposite leaves, blades that are hispidulous and 3-nervate from the base; thickened cypselas with longitudinal ridges, wings up to 0.8 mm wide and margins between the awns ciliate. These specimens may be hybrids between *D. lippioides* and *D. vestitum.*

Additional specimens examined: BRAZIL. **Bahia:** Correntina, Fazenda Jatobá, between 13-14^{0}S and 45^{0}45'-46^{0}15'W, 4 Mar 1991, *Viollati et al. 238* (IBGE, UB). **Distrito Federal:** Brasília, 29 Jan 1963, *Cabrera 15660* (M); *Cabrera 15626* (M); 15 Nov 1958, *Pereira & Pabst 4691* (F); 16 Mar 1959, *Heringer 6644* (SP); ca. 46 km N of Brasília to Vila Buritis, 19 Jan 1980, *King & Almeda 8224* (M, UB); W of Setor Industrial, 1100 m, 27 Nov 1965, *Irwin et al 10720* (NY); S of Brasília, 975 m, 8 Dec 1965, *Irwin et al. 11112* (NY, UB); Barra Alta, E of Córrego São Gonçalo, 15^{0}48'S, 47^{0}31'W, 950 m, 19 Feb 1981, *Kirkbride 3891a* (F, NY, SP,UB); Rod. BR-20, km 16, CPAC-EMBRAPA, 7 Feb 1980, *Kirkbride 1110* (HUFU, UB); Campus Universidade de Brasília, 16 Feb 1986, *Souza s.n.* (UB); Vic. University of Brasília, 20 Jan 1980, *King & Almeda 8230* (G, M); Chapada da Contagem, 13 Feb 1994, *Hatschbach & Silva 60476* (Z); Chapada da Contagem, 20.5 km NW of television tower, 24 Jan 1980, *J. H. Kirkbride & G. Kirkbride 3098* (F, UB); Rod. To Brasilândia, ca.1 km from trevo with BR-60, 15^{0}35'S, 47^{0}57'W, 10 Feb 1988, *Pirani et al. 2113* (NY); Brasília, Catetinho, 20 Mar 1964, *Pereira 9016* (HB); Horto do Guará, 7 Jan 1961, *Heringer 7830* (HB, UB); N end of Lagoa Paranoa, 14 Mar 1966, *Irwin et al. 13950* (NY, UB*)*, Parque Ecológico Norte, 26 Feb 1999, *Moraes & Calago 390* (UEC); Parque Nacional de Brasília, 4 Feb 1992, *Barros et al. 2223* (IBGE); Headquarters of IBGE, 28 Feb 1976, *Heringer 15458* (HB); 2 km from trevo Colorado to Brazlândia, 16 Mar 2001, *Moraes 569* (UEC); 17 Mar 2001, *Moraes & Almeida 578* (UEC); 4 km from trevo Colorado to Brazlândia, 16 Mar 2001; 19 Mar 2001, *Moraes 585* (UEC); *Moraes 586* (UEC); Vargem Bonita, Jan 1962, *Heringer 8864* (B, UB); Riacho Fundo, Fazenda Sucupira, 26 Feb 1999, *Moraes & Calago 382* (UEC); Taguatinga, 20 Jan 1977, *Heringer 16731* (IBGE). **Goiás:** Chapadão do Céu, Parque Nacional das Emas, 17^{0}49'-18^{0}28'S, 52^{0}39'-53^{0}10'W, 3 Jan 1999, *Batalha 2592* (UEC); 1 Feb 1999, *Batalha 2783* (UEC); 8 Mar 1999, *Batalha 2984* (UEC); 1 May 1999, *Batalha*

3306 (UEC); 10 km W of Cristalina, 1200 m, 5 Mar 1966, *Irwin et al. 13 556* (NY); 13 km N of Cristalina, 13 Feb 1981, *King & Bishop 8951* (F, G, M, UB); 2 km S of Cristalina, 22 Jan 1980, *King et al. 8256* (UB); vic. Dois Irmãos, on BR-414, $15^0$20'S, $48^0$39'W, 3 Mar 1978, *Lima 26* (HRB); Luziania, 13 Jan 1967, *Barroso s.n.* (UB); vic Luziania, 25 Jan 1981, *Heringer 18198* (IBGE, UB); Planaltina, km 5-10 on road DF-345, 11 Feb 1990, *Hatschbach & Nicolack 53794* (C, NY, Z); vic. Portelandia, 15 Feb 1974, *Hatschbach 34239* (C); Vale S. Marcos, 12 Jan 1967, *Duarte 10121* (NY). **Mato Grosso:** Cuiabá, BR 364, km 113, 11 Feb 1975, *Hatschbach et al. 36035* (NY). **Minas Gerais:** ad Caldas (protologue), São Paulo, Canna Verde, 18 Feb 1849 (label), *Regnell III n. 770* (S, **syntype of *O. lippioides***); Alpinópolis, 17 Feb 1983, *Dac et al. s.n.* (UEC); 35 km from Piumhi to Araxá, 850 m, 21 Feb 1978, *Shepherd et al. 7108* (UEC); Parque Nacional da Serra da Canastra, 1400m, *Shepherd et al. 7181* (UEC); São Roque de Minas, $20^0$10'S, $46^0$39'W, ca. 1396 m, 13 Jul 1997, *Lombardi 1833* (BHCB); road to Sacramento, Km 11, 22 Feb 1994, *Romero & Nakajima 673* (HUFU); Km 45, 22 Feb 1994, *Romero & Nakajima 695* (HUFU); Guarita de Sacramento, 6 Dez 1994, *Romero & Nakajima 1456* (HUFU); Garagem de Pedras, 12 Jan 1995, *Romero et al. 1773* (HUFU); Uberaba, road BR-50, near Rio Laranjinha, 22 Jan 1988, *Hatschbach & Cordeiro 51750* (C, MO, NY, Z); Uberlândia, campo de aviação, 7 Feb 1947, *Macedo 949* (SP). **São Paulo:** Jundiaí, *Burchell 4900* (photo-K at UEC, photos: F and RB, **syntype of *O. lippioides***).

Dimerostemma myrtifolium (Chodat) M. D. Moraes, Bot. J. Linn. Soc., "submitted".

Verbesina myrtifolia Chodat, Bull. Herb. Boissier 2 (2): 393. 1902. *Zexmenia myrtifolia* (Chodat) Hassl., Repert. Spec. Nov. Regni Veg. 14: 180. 1915. *Angelphytum myrtifolium* (Chodat) H. Rob., Proc. Biol. Soc. Wash. 97 (4): 968. 1984. TYPE: PARAGUAY. In campo pr. Ipé hu, Sierra de Maracayú, Oct, *E. Hassler 4991* (HOLOTYPE probable at G-n.v., ISOTYPES F, K-n.v., F (photo), photo-K and photo-US at UEC). (Fig. 1 L, Fig. 2 J, Fig. 3 F)

Basally woody *perennial herbs* or *subshrubs* (0.3-) 0.5-0.7 (-1.5) m tall, mostly cespitose, from a xylopodium. *Leaves* alternate throughout or sometimes proximally opposite; *petioles* up to 3 mm long; *blades* 2.7-4.5 x 1-2 cm, subcoriaceous, elliptic or sometimes obovate, cuneate at base, shortly acuminate and mucronulate at apex,

sparsely serrulate, both surfaces appearing subglabrate as the trichomes are so small, appressed, sparsely and minutely scabridulous. *Phyllaries* the outer 9-12.5 x 2.5-4 mm, panduriform or elliptic beyond a short oblong base, proximally indurate, the inner 8-11 x 3-3.5 mm, panduriform to oblong to obovate. *Pales* 7.5-9 x ca. 1 mm when folded, subulate. *Ray florets* fertile, tube 1.5-2 mm long, lamina 9-15 x 4-7 mm, oblong, glabrous or with a few trichomes abaxially. *Disc florets* with corollas 4-6 mm long, lobes abaxially glabrous, conspicuously thickened at tip. *Cypselas* 5-6 x 2.5-3 mm, the peripheral trigonous, 3-winged, 3-awned, the inner laterally flattened, wings ca. 2 mm wide; *pappus* awns 3-5 mm long, very broad at base, the longest ca. the same or at least not less than ¾ the length of the cypsela body, crown 0.5-2 mm high, sturdy, usually partially fused to the body (less than 1/3) with erose, fimbriolate margins.

Distribution, habitat and phenology: Mato Grosso do Sul and adjacent Paraguay. Found growing on sandy soils in cerrado, campo-cerrado and campo, with flower from December to March.

Dimerostemma myrtifolium shares overall shape of cypsela with *D. arnottii* and *D. reitzii* (Fig. 3 D - F), but differs from both in wider cypselas and in leaves appearing subglabrate as the trichomes are very appressed, sparsely and minutely scabridulous .

Additional specimens examined: BRAZIL. **Mato Grosso do Sul:** rd. MT-642, 20 km L of Amambai, 16 Dec 1984, *Hatschbach & Callejas 47299* (F, G, MBM); Coronel Sapucaia, corredor international, $23^0$19'S, $55^0$33' W, 27 Mar 2001, *Moraes et al. 619* (UEC); 15 km L of Iguatemi, rd. MS-295, 7 Feb 1993, *Hatshbach et al. 58625* (MBM, Z); 8 km of Iguatemi to Eldorado, $23^0$40'S, $54^0$29'W, 27 Mar 2001, *Moraes et al 625* (TEX, UEC).

PARAGUAY. Amambay, ca. 30 km S of Capitán Bado, Ñunguazú, Ybycuí, 5 Feb 1982, Fdez. *Casas & Molero 5999* (MO).

Dimerostemma oblongum (Gardner) M. D. Moraes, comb. nov.

Serpaea oblonga Gardner, in Hooker, London J. Bot. 7: 395. 1848. *Aspila oblonga* (Gardner) Baker, in C. Martius, Fl. Bras. 6 (3): 198. 1884. TYPE: BRAZIL. Minas Gerais, in campis ditionis Diamantinae, 1941, *Gardner 4928* (HOLOTYPE: K-n.v., photo-K at UEC). (Fig. 2 G)

Basally woody *perennial herbs* or *subshrubs* to ca. 1 m high, xylopodium not seen. *Leaves* opposite throughout; *petioles* up to 1 cm long; *blades* 6-8 x 3-3.5 cm, coriaceous, rigid, oblong or oblong-elliptic, obtuse to very shortly attenuate at base, very shortly acuminate to acute at apex, margins toothed, adaxial surface scabrous, asperous, bullate, the abaxial pilose, prominently reticulate. *Phyllaries* the outer 7-9 (-16) x 6-10 mm, mostly smaller than the inner, erect, not surpassing the disc, elliptic to obovate, constricted at base, rounded and mucronulate at apex, the inner 9-12 x 3-6 mm, spatulate to oblong-obovate and more scarious. *Pales* 11-12 x ca. 1 mm when folded, with rounded tip up to 2 mm long. *Ray florets* sterile, tube 1.5-2 mm long, lamina 16-19 x 5-7 mm, oblong to elliptic, sparsely setulose abaxially. *Disc florets* with corollas 5.5-6 mm long, lobes with a few trichomes abaxially. *Cypselas* 6-6.5 x ca. 3 mm, laterally flattened, wings up to ca. 2 mm wide; *pappus* with awns 4-5 mm long, broad at base, the longest awns are mostly ca. one half or less than ¾ of the cypsela body length, crown ca. 1.5 mm high, partially fused to the cypsela body (less than 1/3), with laciniate margins.

Distribution, habitat and phenology: Restricted to cerrado of Minas Gerais, near 15^0S and 44^0W, on gravelly slopes at 1100 m. Collected with flowers in February.

This species is distinguished in having rigid, coriaceous, oblong or oblong-elliptic blades (Fig. 1 E) and mostly outer phyllaries shorter than the inner, erect and with rounded apex. Some especimens of *Dimerostemma pseudosilphioides* have rigid leaves, but the blades in this species are lanceolate to ovate never oblong (Fig. 1 I).

When proposing *Dimerostemma oblongum* – treated as feminine (*D. oblonga*) - Barroso (Sellowia 26: 105. 1975) cited the combination of Baker (in C. Martius, Fl. Bras. 6

(3): 198. 1884) and thus failed to cite the actual basionym of Gardner (in Hooker, London, J. Bot. 7: 395. 1848). As the Art. 33.6, Ex. 11 of the Saint Louis Nomenclatural Code is parallel to this situation, the combination of Barroso must be treated accordingly as invalid. Therefore, we are here validating the combination of *D. oblongum*.

Additional specimens examined: BRAZIL. **Minas Gerais:** ca. 33 km NE of Francisco de Sá, rd. to Salinas, 1100 m, 11 Feb 1969, *Irwin et al. 23093* (RB).

Dimerostemma pseudosilphioides (Hassl.) M. D. Moraes, Bot. J. Linn. Soc., "submitted".

Zexmenia pseudosilphioides Hassl., Repert. Spec. Nov. Regni Veg. 14: 263. 1916.

Angelphytum pseudosilphioides (Hassl.) H. Rob., Proc. Biol. Soc. Wash. 97 (4): 968. 1984. TYPE: PARAGUAY. Paraguaria Centralis, in regione lacus Ypacaray, May 1913, *E. Hassler 11721* (LECTOTYPE here selected: NY; ISOLECTOTYPES: BM, F (fragment), K-n.v., MO, UC-n.v., US-n.v., Z, photo-B at F, MO and NY, photo-K and photo-US at UEC). (Fig. 1 I, Fig. 2 I, Fig. 3 P)

Z. pseudosilphioides Hassl. f. *discolor* Hassl., Repert. Spec. Nov. Regni Veg. 14: 264. 1916. TYPE: PARAGUAY. Gran Chaco, Santa Rita (protologue), Cordillerae Centralis, in regione collium Cerros de Paraguary, Dec 1900 (label), *E. Hassler 6551* (HOLOTYPE: G-n.v, ISOTYPES: F, UC-n.v.)

Coarse, robust *subshrubs* 1.5-2 m high, from a xylopodium. *Leaves* opposite; *petioles* 3-8(-10) mm long; *blades* 4-8.5(-10) x (1.2-)2.5-3.5(-4.5) cm, mostly rigid and brittle when dried, lanceolate to ovate, shortly attenuate, sometimes very shortly attenuate to rarely truncate at base, acuminate to shortly acuminate at apex, margins serrate, adaxial surface scabridulous to strigose or sericeous, the abaxial paler, strigillose, both surfaces with larger trichomes, especially along the veins, 3-nerved above the base. *Phyllaries* the outer 8-22 x 3-6.5 mm, elliptic to oblong or lanceolate to ovate, slightly constricted and indurate at base, the inner 8-9 x 3-4 mm, ovate to oblong-obovate or elliptic, constricted and indurate at base. *Pales* 7-9 x ca. 1 mm when folded, with subulate or triangular tip up to 2

mm long. *Ray florets* fertile, tube 2-3 mm long, lamina 9.5-19 x 4-8.5 mm, oblong, sometimes obovate to elliptic, abaxially setulose. *Disc florets* with corollas 4-5.5 mm long, lobes glabrous or setulose abaxially. *Cypselas* 3-6 x 1.5-3 mm, the peripheral trigonous, 3-winged, 3-awned or sometimes thickened, subquadrangular, wingless and awnless, the inner slightly flattened, symetrically winged with wings 0.2-1.5 mm wide, obscurely ciliate distally on the opposite side of pale; *pappus* 2-awned, awns 1.2-4 mm long, with relatively narrow, slender bases, the longest mostly less than ¾ the length of the cypsela body, crown 0.2-1.5 mm high, partially fused to the body (1/3 or less) with fimbriolate margins.

Distribution, habitat and phenology: Reported from Paraguay and adjacent Brazilian State of Mato Grosso do Sul, between the coordinates 19^0-25^0S and 55^0-61^0W. Collected with flowers from December to May at wood edges, in dry thorn forest or on rocky hillsides inside cerrado-forest transition.

Dimerostemma pseudosilphioides resembles mostly those specimens of *D. apense* with small leaves, but differs primarily in pales with subulate or triangular tip up to 2 mm long – Fig. 3 P (vs. rigid, linear and pungent tip up to 3.5 mm long – Fig. 3 B).

Additional specimens examined: BRAZIL. **Mato Grosso do Sul:** Bonito, Fazenda Formoso, ca. 8 km from farm house to spring of Rio Formoso, $21^0$15'S, $56^0$38'W, 3 Apr 2001, *Moraes et al. 630* (UEC); 33 km from Porto Murtinho to Jardim, $21^0$44'S, $57^0$34'W, 4 Apr 2001, *Moraes et al. 632* (UEC), 5 Apr 2001, *Moraes et al. 634* (UEC).

PARAGUAY. **Caaguazu:** Coronel Oviedo – Barrio Azucena, 28 May 1985, *Bordas 4124* (CTES). **Caazapa:** Tavai, $26^0$10'S, $55^0$20'W, 17 May 1989, *Ortiz 1252* (MO). **Boqueron:** Filadelfia, $22^0$20'S, $60^0$05'W, 8 Jun 1983, *Hahn 1426* (MO); 25 km S of Línea 10, 26 May, 1994, *Degen & Mereles* 3215 (CTES); Neuland, Parque Vale Natural, $22^0$34'S, $60^0$6'W, 17 Jan 1993, *Perez et al. 2711* (CTES). **Central:** Trinidad, Asuncion, Jardin Botánico Y Zoológico, $25^0$20'S, $57^0$28'W, Mar 1991, *Perez 882* (MO). **Cordillera de Altos:** Dec 1900, *Hassler 3574* (NY, **syntype of *Z. pseudosilphioides***). **Cordillera Centralis:** Cerros de Paraguary, Dec 1900, *Hassler 6551 (*F, **syntype of *Z. pseudosilphioides***). **Chaco:** Ad. Ripam Occidentalem flum. Paraguay, $23^0$20'-$23^0$30'S, Jan 1903,

Hassler 2901 (BM, **syntype of *Z. pseudosilphioides***); 2 km N of cruce Lagerenza, 19^{0}59'S, 60^{0}3'W, 15 Apr 1997, *Mereles 6614* (CTES), 17 Apr 1997, *Mereles 6629* (CTES). **Nueva Asuncion:** Parque Nacional Tte. Enciso, 21^{0}10'S, 61^{0}35'W, 10 Jan 1984, *Hahn 1898* (MO). **Paquari:** Lago Ypoa, 25^{0}57'S, 57^{0}24'W, 26 Nov 1989, *Basualdo & Ortiz 2591* (CTES). **Presidente Hayes:** Villa Hayes, 21 Mar 1985, *Bordas 3797*. **San Pedro:** Alto Paraguay, Primavera, 24 Jun 1956, *Woolston 693* (CTES, NY, S). **Villarica:** Mar 1930, *Jorgensen 4274* (CTES).

Dimerostemma reitzii (H. Rob.) M. D. Moraes., Bot. J. Linn. Soc., "submitted". *Angelphytum reitzii* H. Rob., Proc. Biol. Soc. Wash. 97 (4): 968. 1984. TYPE: BRAZIL. Paraná: Guarapuava, Fazenda 3 Capões, campo seco, 19 Jan 1968, *G.Hatsbach 18327* (HOLOTYPE: MBM; ISOTYPE: US-n.v., photo-US at F, G, UEC). (Fig. 1 S, Fig. 2 M, Fig. 3 E)

Angelphytum hatschbachii H. Rob., Proc. Biol. Soc. Wash. 97 (4): 967. 1984. *Dimerostemma hatschbachii* (H. Rob.) M. D. Moraes, Bot. J. Linn. Soc., "submitted". SYNTYPES: BRAZIL. Mato Grosso do Sul: Ponta Porã, 30 km O, campo limpo, 800 m, 11 Fev 1983, *G. Hatschbach 46131* (HOLOTYPE: MBM; ISOTYPES: C, US-n.v., Z, photos-US at F, G, UEC).

Zexmenia arnottii (Baker) Hassl. var. *virgata* Hassl. f. *angustissima* Hassl., in Repert Spec. Nov. Regni Veg. 14: 270. 1919. SYNTYPES: PARAGUAY. Punta Porá (protologue), In altaplanitie et declivibus Sierra de Amambay, Dec 1907/1908 (label), *Hassler 9857* (F and probable at G-n.v.); Alto Parana, *Fiebrig 6253* (probable at G-n.v.). Lectotypification is deferred until both syntype collections are examined.

Basally woody *perennial herbs* or *subshrubs* 40-90 cm high, mostly cespitose from a xylopodium. *Leaves* alternate; *blades* 1.2-2.7 x 0.1-0.4 cm, subcoriaceous, linear to very narrowly oblong-elliptic; *sessile* or *subsessile*, cuneate at base, very shortly acuminate or sometimes obtuse, mucronulate at apex, margins revolute or slightly so, both surfaces scabrous, one-nerved, not subpinnately netted distally or throughout. *Phyllaries* the outer 5-11.5 x 1.5-2.5 mm, linear to narrowly lanceolate, proximally indurate, the inner 6.5-9 x 2-2.5 mm, narrowly panduriform to oblong or oblanceolate. *Pales* 8-8.5 x ca. 1 mm when

folded, subulate. *Ray florets* fertile, tube 1-2 mm long, lamina 8.5-13 x 3.5-5.5 mm, oblong to elliptic or oblanceolate, sparsely setulose abaxially and proximally. *Disc florets* with corolla 4.5-5 mm long, lobes abaxially glabrous or with a few trichomes. *Cypselas* 3.8-4.5 x ca. 2 mm, the peripheral trigonous, 3-winged, 3-awned, the inner laterally flattened, wings up to 1.2 mm wide, ciliate especially on the opposite side of pale; *pappus* with awns 2-5.5 mm long, mostly unequal, the longest ca. of the same length of the cypsela body or longer, broad to very broad at base, crown 0.5-1 mm high, almost completely fused to the body (more than 2/3) with minutely lacerate to entire margins, mostly with squamelloid processes, partially fused to the awns.

Distribution, habitat and phenology: Paraguay and the adjacent Brazilian states of Mato Grosso do Sul, Paraná and Santa Catarina. Found in campo, growing on sandy or stony soils. Collected with flower from December to March.

Robinson (1984) considered *Angelphytum hatschbachii*, occurring in Mato Grosso do Sul and neighbouring Paraguay, distinguished from *A. reitzii*, distributed in the adjacent southern Brazilian States of Paraná and Santa Catarina. The type specimens of *A. hatsbachii* show smaller leaves and heads than the others specimens examined, but besides the size of these structures there is no consistent differences in any other character. *Dimerostemma reitzii* shares similar cypselas with *D. arnottii* (Fig. 3 D - E) and is very closely resembles some specimens of *D. arnottii* with short and narrow leaves (Fig. 1 F), see commentaries under the latter.

Additional specimens examined: BRAZIL. **Mato Grosso do Sul:** 9 km W of Caparaó, 22^{0}35'S, 54^{0}55'W, 19 Jan1979, *Krapovickas & Cristóbal 34330* (CTES). **Paraná:** Guarapuava, Fazenda 3 Capões, 24 Feb 1971, *Hatschbach 26491* (S); 85 km SW of Guarapuava, Fazenda Reserva, 800-1000m, 13 Mar 1967, *Lindeman & Haas 4814* (NY). **Santa Catarina:** ca. 3 Km N of Abelardo Luz, 9 Mar 2000, *Moraes 432* (TEX, UEC).

PARAGUAY. **Amambay:** Cordillera de Amambay, 13-15 Km S of rd. 5, Cerro Corá, Colonia Picada Lorito, 11 Dec 1997, *Schinini & Dematteis 33740* (CTES); 30 km L of Pedro Juan Caballero, $21^0$45'S, $55^0$45'W**,** 15 Dec 1983, Callejas et al. 1938 (NY, RB).

Dimerostemma retifolium (Baker) S. F. Blake, Contr. Gray. Herb. n.s. 52: 11. 1917. ?*Viguiera retifolia* Sch. Bip. ex Baker, in C. Martius, Fl. Bras. 6 (3): 223. 1884. TYPE: BRAZIL. Mato Grosso, fields along Rio Pardo, *Riedel s.n.* (HOLOTYPE: G-n.v. (fragment), K-n.v., photo-K at UEC).

Angelphytum matogrossense G. M. Barroso, Bol. Soc. Argent. Bot. 19: 9. 1980. TYPE: BRAZIL. Mato Grosso: mun. Campo Grande, Rod. Br. 163 prox. a Agua Ruim, Cerrado, 14 Aug 1970, *G. Hatschbach 24639* (HOLOTYPE: RB; ISOTYPE: MBM). (Fig. 1E, Fig. 3H)

Basally woody *perennial herbs* or *subshrubs* 0.5-1.70 m high, xylopodium not seen. *Leaves* alternate; *petioles* up to 5 mm long; *blades* 4.5-8 x 2.5-3.5 cm, coriaceous, elliptic to oblong-elliptic or sometimes ovate, cuneate at base, obtuse or sometimes rounded and mucronate at apex, margins minutely toothed distally, both surfaces grayish-green, appressed and densely scabridulous, sparsely so along the veins and prominently reticulate. *Peduncles* stout; *heads* campanulate; *phyllaries* the outer 9-15 x 3-5,5 mm, oblong to elliptic or obovate, constricted and indurate at base, the inner 6-8 x 2-3 mm, oblong, not or slightly constricted at base to oblong-obovate and more scarious. *Pales* 6-8 x ca. 1.2 mm when folded, tip obtuse to rounded, reflexed, up to ca. 1 mm long. *Ray florets* absent. *Disc florets* with corollas 4-5 mm long, lobes glabrous. *Cypselas* 5-6 x 2-2.5 mm, the peripheral trigonous, 3-winged, 3-awned, the inner laterally flattened, wings 1-1.5 mm wide; *pappus* with awns 2-3.5 mm long, broad to very broad at base, the longest awn mostly ca. one half or less than ¾ of the cypsela body length, crown 0.5-1(-1.8) mm high, partially fused to the cypsela body (less than 1/3) with lacerate margins.

Distribution, habitat and phenology: it is a rare plant, growing in campo-cerrado of Mato Grosso do Sul and adjacent Goiás. In the latter it was found associated with *Attalea* sp., a small palm tree ca. 2 m high. Collected in flower from August to November, earlier than most species in the genus (with old heads in May).

We treat here *Angelphytum matogrossense*, the type of the genus, as synonym of *Dimerostemma retifolium*. The original description of *Viguiera ? retifolia* (*=Dimerostemma retifolium*) was based on a single specimen with immature cypselas. Thus, Baker (1884) was unable to observe the trigonous, 3-winged peripheral cypselas, which were not yet developed, and was unsure about the eradiate state of the heads. These characters, which were neither mentioned by Baker (1884) nor Blake (1917), agreed with the establishment of *Angelphytum* on the basis of *A. matogrossense* by Barroso (1980). The later author stressed both characters to differentiate her new genus from *Dimerostemma* (with peripheral sterile florets, in consequence not developing the trigonous, 3-winged peripheral cypselas) and *Zexmenia* La Llave & Lex. (with rayed heads).

Dimerostemma retifolium is similar to *D. brasilianum* in eradiate heads but is easily recognized by the coriaceous leaves, which are alternate, mostly elliptic to oblong-elliptic and by the very distinctive indument, which is appressed and densely scabridulous.

Additional specimens examined: BRAZIL. **Goiás:** Chapadão do Céu and Mineiros, Parque Nacional das Emas, $17^0$49'-$18^0$28'S, $52^0$39'-$53^0$10'W, 3 Nov 1998, *Batalha 2246* (UEC); 7 May 2001, *Batalha & Martins 4027* (UEC). **Mato Grosso do Sul:** Camapuã, Capão Redondo, 26 Aug 1973, *Hatschbach 32374* (C, NY, RB, Z); rd. from Presidente Prudente to Campo Grande, Km-156, 9 Jun 1976, *Leitão Filho et al. 2082* (UEC).

Dimerostemma vestitum (Baker) S. F. Blake, Contr. Gray. Herb. n.s. 52: 11. 1917. *Oyedaea vestita* Baker in Martius, Fl. Bras. 6 (3): 207. 1884. TYPE: BRAZIL. Goiás: in campo near the town of Goyaz, *Burchell 6815* (LECTOTYPE here selected: K-n.v., photo-K at UEC). Fig. 1 A, Fig. 2 A, Fig. 3 K)

Basally woody *perennial herbs* or *subshrubs* to ca. 1 m high, mostly cespitose, from a xylopodium. *Leaves* mostly alternate, sometimes opposite at the base or throughout or yet shoots may be opposite and alternate leaved in the same plant; *petioles* up to 5 mm long; *blades* 2-4.5(-6.5) x 2-4.5(7) cm, chartaceous, ovate to broadly ovate or orbicular, cordate or sometimes subcordate or subtruncate at base, rounded to rarely obtuse at apex, margins crenate-serrulate, both surfaces mostly tomentose or subtomentose, rarely pilose-strigillose, usually soft to the touch, the abaxial dull cinereous, more densely indumented, 3-nerved from near to well above the base and reticulate. *Heads* in loose dichasiiform associations of 2-3 at the ends of primary and axillary shoots or sometimes solitary; *peduncles* stout, mostly with leaves nearly or at the bases of the heads, rarely somewhat elongated; *phyllaries* the outer 12-30 x 9-22 mm, elliptic or sometimes ovate, strongly indurate at base, the inner 6-20 x 4-15 mm, like the outer but slightly constricted at base to oblong and more scarious. *Pales* 8.5-10 x 1-2 mm when folded, with subulate or triangular tip 1-1.5 mm long. *Ray florets* sterile, tube 1.5-2.5 mm long, lamina 13.5-21 x 3-5 mm, elliptic to oblong-elliptic or oblong, densely setulose abaxially, 2-3 lobes shallowly ou deeply cut. *Disc florets* with corollas 5-6 mm long, lobes abaxially setulose. *Cypselas* 3-4 x 1.8-2 mm, thickened, subquadrangular, with 1(-3) longitudinal ridges, smooth, mostly setulose, rarely finely and sparsely tuberculate, wingless or wings reduced to a narrow, often paler margins, ciliate on the margin opposite the pale; *pappus* with awns 0.5-2.5 mm high, relatively broad at base, mostly unequal, the longest being ca. one half or less than ¾ of the cypsela body, crown reduced to a ciliate or rarely entire margin.

Distribution, habitat and phenology: Reported from campo and cerrado in Distrito Federal, Goiás and adjacent Minas Gerais, on red or sandy clay soils at 800 to 1200 m. Collect in flower from December to April.

Some specimens from Distrito Federal, where *D. vestitum* grows sympatrically with *D. lippioides* (e.g. *Moraes 590* and *592*, UEC), have leaves that are proximally opposite and distally alternate, with blades that are tomentose and 3-nervate from the base. The cypselas are slightly flattened and with longitudinal ridges, the wings are narrow, not wider then 0.8 mm, and the margin between the unequal awns are entire (*Moraes 592*) or ciliate (*Moraes 590*). These specimens may be hybrids between *D. vestitum* (Fig. 1 A and Fig. 3 K) and *D. lippioides* (Fig. 1 B and Fig. 3 J) See also commentaries under *D. lippioides*.

Additional specimens examined: BRAZIL. **Distrito Federal:** Brasília, 19 Mar 1964, *Pereira 8990* (HB, UB);Reserva Biológica de Águas Emendadas, 2 Mar 1989, *Filgueiras & Porto 1866* (IBGE); Centro Olimpico da UnB, $15^0$35'S, $47^0$52'W, Nov 1993, *class UnB 1111* (UB); 46 km N of bridge at Asa Norte to Vila dos Buritis, 19 Jan 1980, *King & Almeda 8219* (M, MO, UB); North side of Vale de Ribeirão Bananal, $15^0$42'S, $47^0$54'W, 1060 m, 18 May 1980, *Kirkbride 3183* (F); Horto do Guará, 20 Jan 1962, *Heringer 8853* (B, UB); E of Lagoa Paranoá, 975 m, 10 Dec 1965, *Irwin et al. 11165* (F, NY, UB); Chapada da Contagem, 31 Jan 1980, *Kirkbride 1042* (UB); Summit of Chapada da Contagem, 1100 m, 14 Jan 1966, *Irwin et al. 11678* (G, NY, UB); *Irwin et al. 11643* (UB); road Brasília to Uruaçu, 15 Dez 1964, *Belém & Mendes 26* (UB); Chapada da Contagem, 19.5 Km NW of Central Brasília, 26 Jan 1980, *King et al. 8319* (UB); road DF-5, 16 Dez 1964, *Belém & Mendes 49* (UB); Reserva Biológica do IBGE, 10 Mar 1992, *Morbeck & Proença 39* (IBGE); 22 Feb 1984, *Moreira 58* (IBGE); $15^0$57'S, $47^0$52'W, 25 Apr 1988, *Silva et al. 591* (IBGE); $15^0$56'S, $47^0$53'W, 1100 m, 27 Mar 1995, *Silva 2497* (IBGE); 10 Jan 1996, *Silva 2858* (IBGE); 20 Dez 1983, *Pereira 888* (IBGE); Planaltina, 64 km from UnB, 27 Jan 1991, *Fontella & de Paula 2717* (HB); Parque Nacional de Brasília, Alto do Milho Cozido, $15^0$53'S, $47^0$56'W, 12 Dez 1990, *Ramos 399, 407, 408* (UB); 5 km N of Brasília to Sobradinho, 27 Jan 1978, *Krapovickas & Cristóbal 33249* (CTES); Riacho Fundo, Fazenda Sucupira, 26 Feb 1999, *Moraes & Calago 383* (UEC); ca. of 2 km from Trevo do

Colorado to Brazlândia, 25 Feb 1999, *Moraes & Oliveira 372* (UEC); ca. of 4 Km from trevo do Colorado to Brazlândia, 25 Feb 1999, *Moraes & Oliveira 373, 374* (UEC); road BR-40 to Valparaíso, 26 Feb 1999, *Moraes & Calago 385, 386, 387* (UEC); Parque Ecológico Norte, 26 Feb 1999, *Moraes & Calago 388, 389* (UEC); 2 km from Trevo Colorado to Brazlândia, 16 Mar 2001, *Moraes 566, 567, 570, 571, 572* (UEC); 4 km from Trevo Colorado to Brazlândia, 19 Mar 2001, *Moraes 591, 593, 595* (UEC). **Goiás:** vic. S. Antonio del Monte, *Sello 1088* (photos: F, MO, RB, **syntype of *O. vestita***) 15 Km N of Corumbá de Goiás, 1150 m, 14 Jan 1968, *Irwin et al. 18597* (F, NY, UB); Serra dos Pirineus, 18 Dec 1995, *Macedo 3484* (NY); 12 km N of Cristalina, 1060 m, 3 Apr 1973, *Anderson 8003* (NY); ca. 10 km W of Cristalina, 1200 m, *Irwin et al. 13556* (UB); vic. Of Cristalina, 6 Mar 1999, *Moraes 406* (UEC); ca. 8 km from Cristalina to Brasília, 6 Mar 1999, *Moraes 409* (UEC); ca. 42 km NE of Formosa, 800 m, 20 Apr 1966, *Irwin et al. 15141* (NY, UB); 20 km SE of Goiás Velho, summit of Serra dourada, 800 m, 20 Jan 1966, *Irwin et al. 11836* (NY, UB, UEC); Serra Dourada, 21 Jan 1967, *Duarte 10267* (HB, UB); Niquelândia, $14^0$20'S, $48^0$25'W, 780 m, 1 Dec 1996, *Fonseca et al. 1423* (IBGE); Niquelândia, $14^0$23'S, $48^0$24'W, 13 Dec 1995, *Fonseca et al.706* (IBGE); ca. 20 km N of Curralinho to Padre Bernardo, $15^0$15'S, $48^0$15'W, 28 Feb 1992, *Filgueiras 2213* (IBGE); ca. 10 km E of Pirenópolis, 1000 m, 15 Jan 1972, *Irwin et al 34157* (NY, UB); Serra dos Pirineus, 1350 m, 7 Dec 1987, *Semir et al. 20511* (UEC); Morro do Frota, 920 m, 10 Dec 1987, *Semir et al. 20068* (UEC); ca. 10 km E of Pirenópolis, 7 Mar 1999, *Moraes 411, 412* (UEC); Vale do Rio S. Marcos, 12 Jan 1967, *Duarte 10141* (HB, UB). **Minas Gerais:** Queimados-Unaí, 20 Jan 1998, Costa s.n. (BHCB); Perdizes, 17 Dec 1994, *Tameirão Neto & Werneck 1293* (BHCB); São Roque de Minas, Parque Nacional da Serra da Canastra, 10 Dec 1996, *Nakajima & Kinoshita 2461* (UEC); Vale dos Cândidos, 27 Jun 1997, *Romero et al. 4320* (HUFU);**Unknown locality:** *Pohl 572* (K-n.v., photo-K at UEC, **syntype of *O. vestita***).

Dimerostemma virgosum H. Rob., Proc. Biol. Soc. Wash. 97 (3): 625. 1984. TYPE: BRAZIL. Mato Grosso do Sul, mun. de Ladário, pantanal, 8 Nov 1982, *J.E. de Paula & C. A. Conceição 1627* (HOLOTYPE: IBGE-n.v., not found; ISOTYPES: Cor (fragment), US–n.v., photo-US at F, G, K, UEC). Fig. 3 R)

Basally woody *perennial herbs* or *subshrubs* to ca. 1 m tall, branches stramineous, xylopodium not seen. *Leaves* opposite; *petioles* up to 1 mm long; *blades* 2-8.5 x 0.6-1.9 cm, length mostly 3-5 times width, submembranous, lanceolate to narrowly lanceolate, shortly attenuate at base, acuminate at apex, margins remotely serrulate, adaxial surface strigillose, the abaxial densely villous, with larger trichomes along the veins. *Phyllaries* the outer 9 x 3.5 mm, oblong-ovate, indurate at base, the inner 5 x 2 mm, oblong-ovate, indurate and constricted at base to oblong-obovate and more scarious. *Ray florets* sterile, tube ca. 1 mm long, lamina 15 x 3 mm. *Disc florets* with corollas ca. 4 mm long. *Pales* 6.5-7 x ca. 1 mm when folded, with rigid acute linear tip up to 2 mm long. *Cypselas* 3-3.5 x ca. 1.5 mm, thickened, subquadrangular, slightly tuberculate at maturity, wings much reduced, up to 0.5 mm wide, slightly asymmetrical being wider on the opposite side of pale; *pappus* awnless, crown reduced to a minutely ciliated margin.

Distribution, habitat and phenology: Restricted to Mato Grosso do Sul, has been collected with flower in November.

Our description of *D. virgosum* is based on the original, an isotype fragment of Cor (with mature cypselas) and photographs of the isotype at US. We have seen no other material. This species is the only member of the genus in which the branches are stramineous. *Dimerostemma virgosum* shares with *D. species nova* and *D. bishopii* similar shape of cypsela (Fig. 3 Q – S). It differs from *D. bishopii* mainly in blades shortly attenuate at base (vs. rounded to truncate or subcordate) and from *D. specie nova* in narrower blades (length mostly 3-5 times width), remotely serrulate margins and densely villous abaxially (vs. length mostly ca. 2 times width, serrate and strigillose).

Dimerostemma species nova M. D. Moraes, sp. nov. (Fig.4). This new species will be valid published in a near future somewhere else.

TYPE: BRAZIL. Mato Grosso do Sul: Miranda, $20^0$7'48"S, $56^0$42'16"W, 24 Mar 2001, *M. D. Moraes*, *J. F. M. Valls*, *R. C. Oliveira* & *G. P. Silva* 613 (HOLOTYPE: UEC; ISOTYPES: G, NY, RB, SP, TEX). (Fig. 3)

(Diagnosis in latin in preparation)

Basaly wood perennial *herbs* or *subshrubs* 0.5-1 m high, branches brownish-green, without xylopodium. *Leaves* opposite; *petioles* 2-7 mm long; *blades* 3.5-9 x 1.5-4 cm, length mostly ca. 2 times width, membranous, ovate to lanceolate, shortly attenuate at base, acuminate or sometimes obtuse and mucronulate at apex, margins serrate, adaxial surface scabridulous, the abaxial strigillose, with scattered larger trichomes on both faces, especially along the veins, 3-nerved above the base, subpinnately netted distally. *Phyllaries* the outer 6-20 x 2-7 mm, elliptic to lanceolate, constricted at base to panduriform, slightly indurate at base, the inner elliptic, slightly constricted at the middle base then enlarged and indurate at the very base to obovate and scarious. *Pales* 5-6.5 x 1-2 mm when folded, carinate-alate, sometimes very broadly alate, with triangular tip 0.5-1 mm long. *Ray florets* sterile, tube 0.5-1 mm, lamina 6-12 x 3.5-4 mm, elliptic to oblong, pratically glabrous, very shallowly 3-lobed. *Disc florets* 3-4.5 mm long, lobes sparsely setulose or glabrous abaxially. *Cypselas* 3-4.2 x 1.5-2 mm, thickened, subquadrangular, densely tuberculate at maturity, mostly wingless or with wings much reduced up to 0.2 mm wide; *pappus* awnless, crown completely enfolded in corky tissue at maturity, appearing reduced to an entire or ciliate margin.

Distribution, habitat and phenology: Reported from the Pantanal of Mato Grosso do Sul near 20^0S – 56^0W, among sandstone outcrops or on clay soils in a seasonally flooded area. Collected with flowers in February/ March.

Dimerostemma species nova resembles *D. bahiense* in similarities of heads and leaves, but differs primarily in sterile ray florets; and resembles *D. bishopii* and *D. virgosum* in thickened, subquadrangular, mostly wingless and awnless cypselas (Fig. 3 Q – S). *Dimerostemma species nova* differs from *D. bishopii* mainly in blades shortly attenuate at base (vs. rounded to truncate or subcordate – Fig. 1D). It differs from *D. virgosum* in wider blades (length mostly ca. 2 times width), serrate margins and strigillose abaxial surface (vs. length mostly 3-5 times width, remotely serrulate and densely villous).

Additional specimens examined: BRAZIL. **Mato Grosso do Sul:** 10 Km N of Rio Verde, 9 Feb 1975, *Hatschbach et al. 35983* (F, NY, S); 51 km W of Miranda on BR-262, 13 Feb 1993, *Hatschbach et al. 59025* (MBM, Z).

Doubtful and excluded names

Zexmenia hieronymi Hassler, Repert Spec. Nov. Regni Veg. 157. 1915. TYPE: ARGENTINA. Inter Arroyo medio et Tomas. Entre Rios, 15 feb 1878, *Lorenttz 1384* (HOLOPTYPE: B, destroyed). The plant figured in the protologue has cypselas with narrow wings and shows affinity in pappus features with *Viguiera* Kunth of the Helianthinae.

Dimerostemma bonplandianum (Gardner) Pruski. This name was applied by Pruski to specimens of *Dimerostemma species nova* from Miranda, *Hatschbach et al.* 59025 at Z and MBM. He labeled this specimen in 1996, but he never published this combination, that would be based on *Viguiera bonplandiana* Gardner, London J. Bot. 7: 399. 1848. TYPE: BRAZIL. Piauhy, in campis apertis inter Samambaia e Retiro, 1839, *Gardner 2218* (LECTOTYPE, designated by Moreira dos Santos, 2001: G; ISOLECTOTYPES: G, W, BM). = *Oyedaea bonplandiana* (Gardner) Benth., Gen. Pl., 2: 374. 1873. = *Aspilia bonplandiana* (Gardner) Blake, Contr. US Natl. Herb. 20: 421. 1921. = *Wedelia bonplandiana* (Gardner) B. L. Turner, Phytologia 72: 391. 1992.

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Robinson H. 1984b. Studies in Heliantheae (Asteraceae). XXXIV. Redelimitation of the genus *Angelphytum.* Proc. Biol. Soc. Wash. 97: 961-969.

FIG. 1. Leaves in *Dimerostemma*. **A.** *D. vestitum* (*Moraes 373*, UEC). **B.** *D. lippioides*(*Moraes 587*, UEC). **C.** *D. brasilianum* (*Moraes 393*, UEC). **D.** *D. bishoppii* (*Moraes & Alvarenga 640*, UEC). **E.** *D. retifolium* (*Batalha & Martins 4027*, UEC). **F.** *D. arnottii* (*Hatschbach 58697*, Z). **G.** *D. arnottii* (*Moraes et al. 618*, UEC). **H.** *D. arnottii* (*Moraes 443*, UEC). **I.** *D. pseudosilphioides* (*Moraes et al. 634*, UEC). **J.** *D. oblongum* (*Irwin et al. 23093*, RB). **K.** *D. humboldtianum* (*Moraes & Oliveira 540*, UEC). **L.** *D. myrtifolium* (*Moraes et al. 619*, UEC). **M.** *D. episcopale* (*Moraes & Aona 449*, UEC). **N.** *D. grazielae* (*Moraes 647*, UEC). **O.** *D. apense* (*Moraes et al. 615*, UEC). **P.** *D. bahiense* (*Moraes & Aona 447*, UEC). **Q.** *D. goyazense* (*Moraes& Alvarenga et al. 636*, UEC). **R.** *D. annuum* (*Moraes et al. 629*, UEC). **S.** *D. reitzii* (*Moraes 432*, UEC). All bars = 1 cm.

FIG. 2. Heads in *Dimerostemma*. **A.** *D. vestitum* (*Moraes 591*, UEC). **B.** *D. lippioides* (*Heringer 15458*, HB). **C.** *D. brasilianum* (*Moraes 393*, UEC). **D.** *D. episcopale* (*Moraes & Aona 449*, UEC). **E.** *D. grazielae* (*Moraes 651*, UEC). **F.** *D. goyazense* (*Moraes & Alvarenga 636*, UEC). **G.** *D. annuum* (*Moraes et al. 629*, UEC). **H.** *D. apense* (*Moraes et al. 615*, UEC). **I.** *D. pseudosilphioides* (*Moraes et al. 634*, UEC). **J.** *D. myrtifolium* (*Moraes et al; 625*, UEC). **K.** *D. humboldtianum* (*Moraes & Oliveira 540*, UEC). **L.** *D. arnottii*

(*Moraes 441*, UEC). **M.** *D. reitzii* (*Moraes 432*, UEC). **N.** *D. bahiense* (*Moraes & Aona 448*, UEC). All bars = 1 cm.

FIG. 3. Disc cypselas and pales in *Dimerostemma*. **A.** *D. annuum* (*Hassler 11030*, NY). **B.** *D. apense* (*Moraes et al. 615*, UEC). **C.** *D. bahiense* (*Moraes & Aona 448*, UEC). **D.** *D. arnottii* (*Moraes 437*, UEC). **E.** *D. reitzii* (*Moraes 430*, UEC). **F.** *D. myrtifolium* (*Moraes et al. 625*, UEC). **G.** *D. oblongum* (*Irwin et al. 23093*, RB). **H.** *D. retifolium* (*Hatschbach 24639*, RB). **I.** *D. brasilianum* (*Moraes 405*, UEC). **J.** *D. lippioides* (*Moraes & Almeida 578*, UEC). **K.** *D. vestitum* (*Moraes & Oliveira 373*, UEC). **L.** *D. humboldtianum* (*Sucre 874,* M). **M.** *D. episcopale* (*Moraes & Aona 501*, UEC). **N.** *D. grazielae* (*Irwin et al. 32779*, NY). **O.** *D. goyazense* (*Heringer 8182*, UB). **P.** *D. pseudosilphioides* (*Hassler 11721*, NY). **Q.** *D. bishopii* (*Silva et al. 4309*, IBGE). **R.** *D. virgosum* (*Paula & Conceição 1627*, COR). **S.** *D. specie nova* (*Moraes et al. 613*, UEC). All bars = 2 mm.

FIG. 4. *Dimerostemma specie nova.* **A.** Flowering branch. **B.** Head. **C.** Ray floret. **D.** Disc floret. **E.** Pale. **F.** Cypsela.

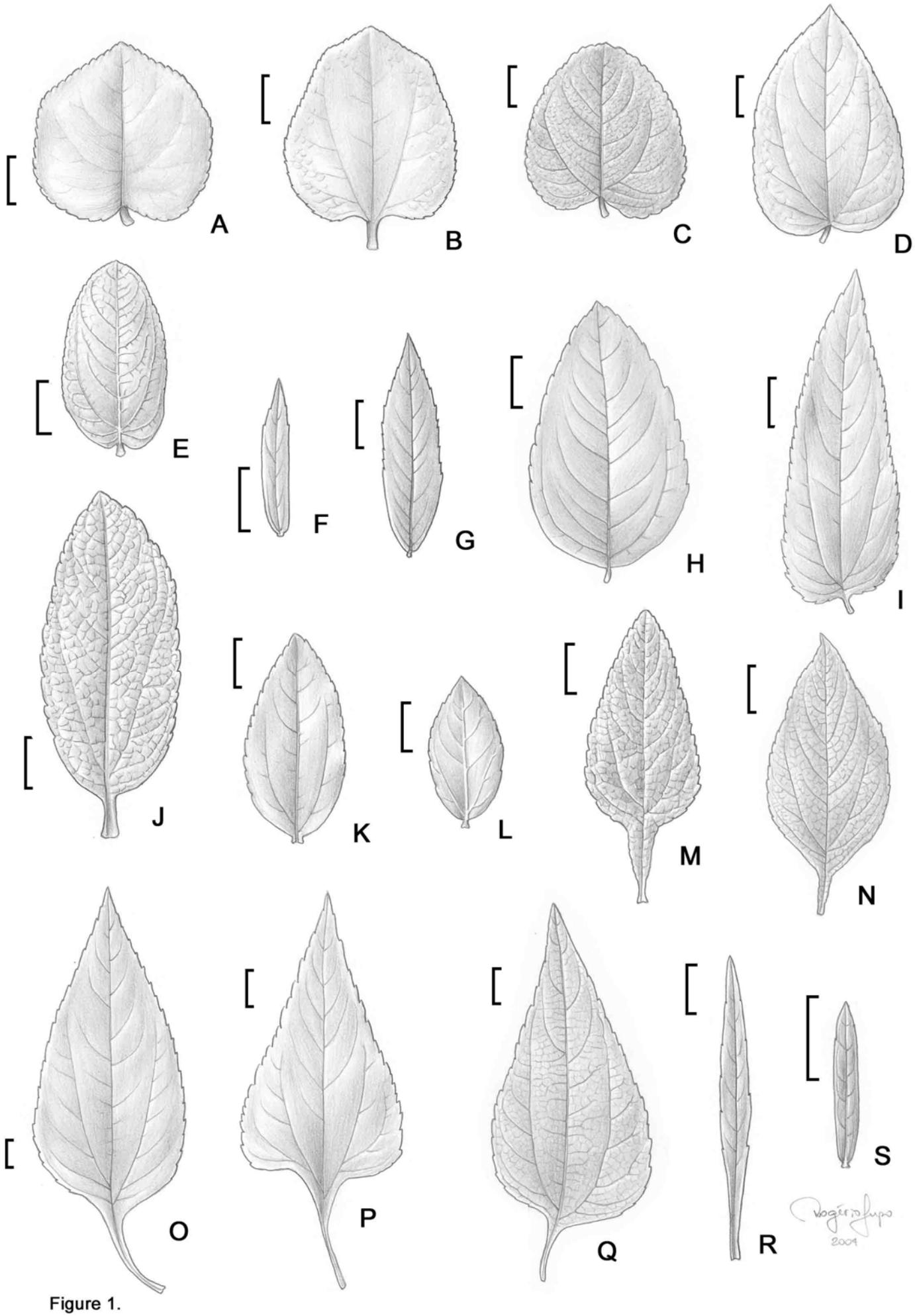

Figure 1.

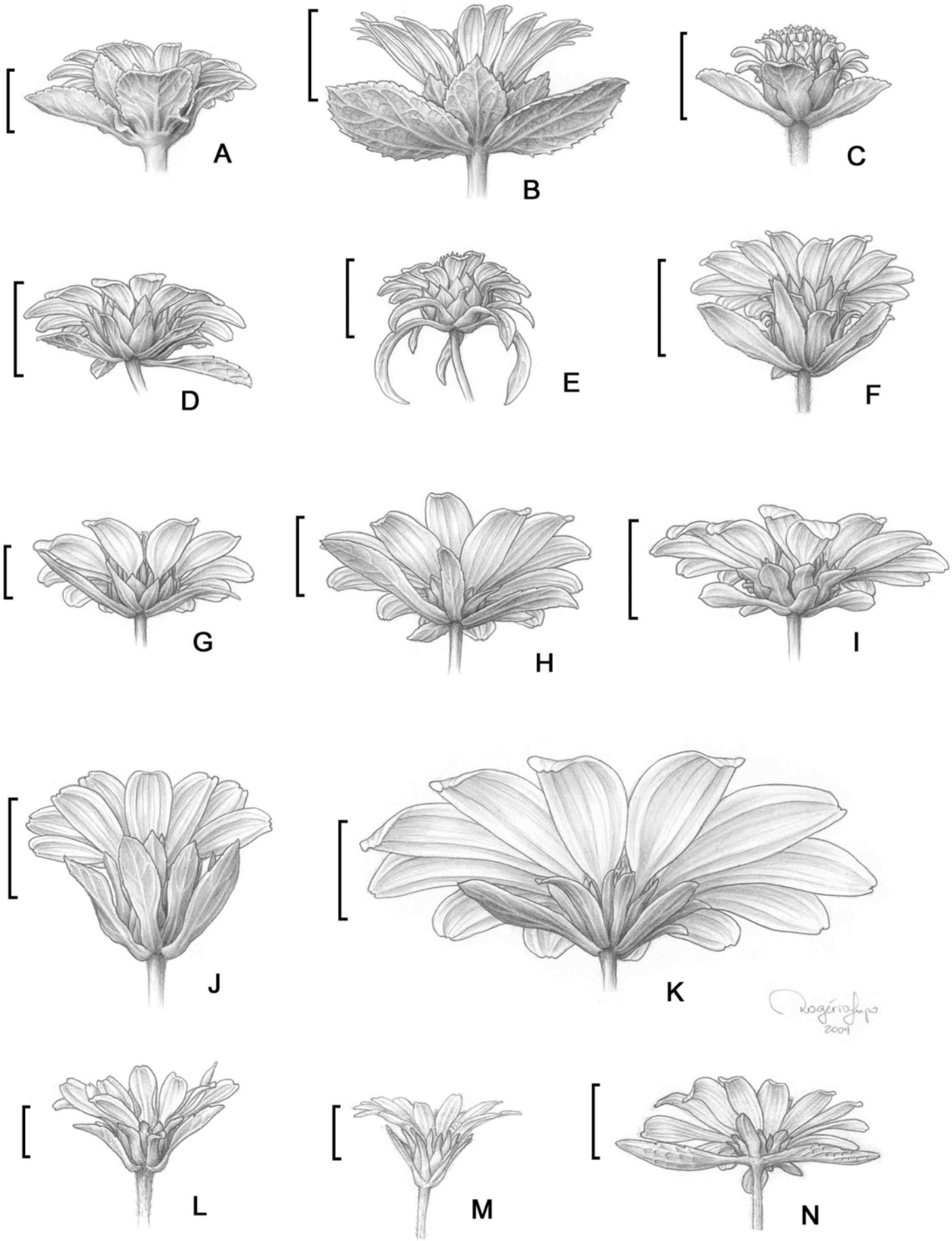

Figure 2.

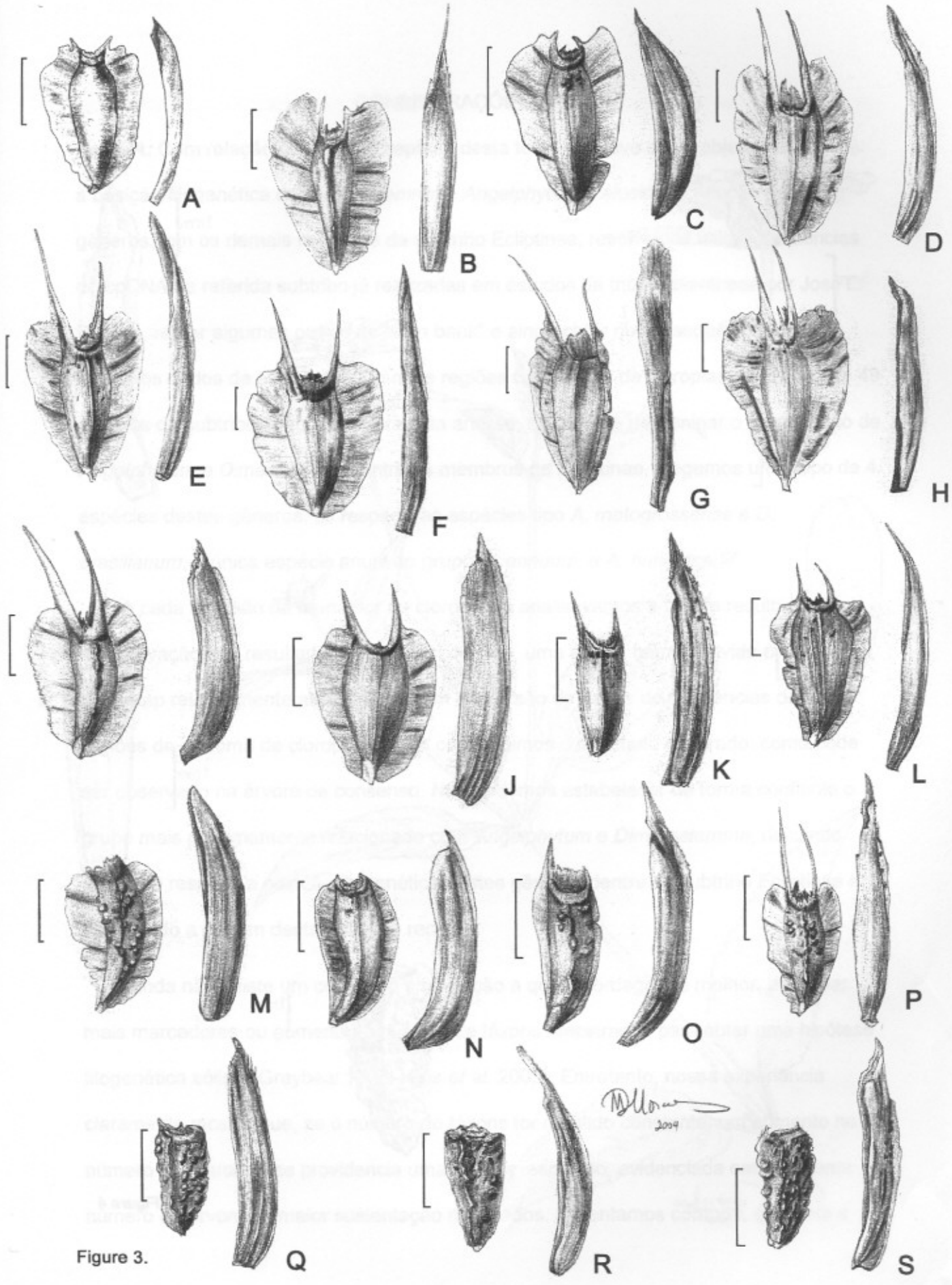

Figure 3.

Figure 4

CONSIDERAÇÕES FINAIS

CpDNA: Com relação ao primeiro capítulo desta tese, que teve como objetivo esclarecer a posição filogenética de *Dimerostemma* e *Angelphytum* e elucidar a relação destes gêneros com os demais membros da subtribo Ecliptinae, resolvemos utilizar seqüências de cpDNA da referida subtribo já realizadas em estudos da tribo Heliantheae por José L. Panero, retirar algumas outras do "Gen bank" e ainda obter novas seqüências. Assim, incluímos dados de seqüências de nove regiões do genoma de cloroplasto para 34 dos 49 gêneros da subtribo Ecliptinae. Para esta análise, que visava determinar o grupo irmão de *Angelphytum* e *Dimerostemma* entre os membros de Ecliptinae, elegemos um grupo de 4 espécies destes gêneros: as respectivas espécies tipo *A. matogrossense* e *D. brasilianum*, a única espécie anual do grupo *D. annuum*, e *A. bahiense*.

A cada inclusão de marcador de cloroplasto analisávamos a árvore resultante para comprovação dos resultados esperados, ou seja, uma árvore bem resolvida com bootstrap relativamente alto. Mesmo com a inclusão de dados de seqüências de nove regiões do genoma de cloroplasto, não conseguimos o resultado esperado, como pode ser observado na árvore de consenso. Não podemos estabelecer de forma confiante o grupo mais proximamente relacionado com *Angelphytum* e *Dimerostemma*, deixando assim de resolver a posição filogenética destes gêneros dentro da subtribo Ecliptinae e elucidando a origem desta radiação recente.

Ainda não existe um consenso em relação a qual abordagem é melhor, adicionar mais marcadores ou aumentar o número de táxons amostrados para obter uma hipótese filogenética sólida (Graybeal 1998; Hillis *et al.* 2003). Entretanto, nossa experiência claramente mostra que, se o número de táxons for mantido constante, um aumento no número de marcadores providencia uma melhor resolução, evidenciada em um menor número de árvores e maior sustentação nos clados. Salientamos contudo, que para a

obtenção de uma resolução fidedigna, o número de táxons deve representar uma boa amostragem do grupo em estudo.

Uma limitação ao nosso estudo foi a dificuldade de obtenção de DNA em quantidade e de boa qualidade para alguns dos táxons da subtribo. Espécimes de herbário, dependendo do estado de conservação, podem providenciar material suficiente para algumas amplificações, mas não o bastante para uma grande quantidade de marcadores. Além disso, geralmente o DNA obtido de espécimes de herbário não é de boa qualidade. Estudos mais amplos, que tenham como objetivo esclarecer a filogenia da tribo Heliantheae e táxons relacionados, requerem trabalho de campo extenso para a coleta de material vegetal para a obtenção de DNA. Como as plantas encontram-se espalhadas pelas regiões dos neotrópicos, esta coleta requer a colaboração de vários pesquisadores trabalhando em conjunto.

Uma abordagem molecular para elucidar a filogenia da tribo Ecliptinae torna-se bastante apropriada devido a homoplasia de caracteres, observada em vários de seus membros. Esta a homoplasia, visualizada por Strother (1991) em seu estudo taxonômico para a subtribo, foi resumida da seguinte maneira “Afinidades ou relações entre todos os gêneros de Ecliptinae ... frequentemente parecem ser reticuladas. Certas expressões de caráter são recorrentes em diferentes combinações entre alguns dos gêneros”. O estudo molecular revelou uma quantidade significante de a homoplasia para caracteres chaves, tradicionalmente utilizados na classificação de Ecliptinae. Por exemplo, a árvore de cpDNA indica que a constrição do ápice da cipsela, uma característica bastante utilizada na separação de gêneros dentro da subtribo Ecliptinae, parece ter evoluído em paralelo várias vezes, pois encontra-se presente em gêneros de diferentes grupos, incluindo o grupo de *Blainvillea*, de *Trigonopterum* e *Sphagneticola*, e ainda o de *Wedelia*. Um outro caráter que tem sido prontamente utilizado na delimitação de grupos dentro de

Heliantheae é a presença ou ausência de flores do disco funcionalmente masculina. Este caráter parece ter evoluído independentemente no mínimo duas vezes na subtribo, uma vez que encontra-se presente em *Baltimora*, *Clibadium*, *Riencourtia* e *Rensonia*, todos aparecendo como linhagens solitárias no clado de Wedelia, e em *Delilia*, membro do clado de *Blainvillea*.

Nosso estudo contribuiu para o esclarecimento das relações filogenéticas de Ecliptinae, mas estudos adicionais com um maior número de táxons e marcadores são necessários para uma melhor compreensão da sistemática e evolução do grupo.

DNA nuclear: Já no que diz respeito ao segundo capítulo desta tese, esperávamos valer-nos do grupo irmão de *Angelphytum* e *Dimerostemma*, resultante da análise dos dados das seqüências de cpDNA. Este grupo irmão seria aplicado como grupo externo em uma segunda análise, que utilizaria seqüenciamento do ITS e ETS para as espécies de *Angelphytum* e *Dimerostemma.* Acreditávamos que a utilização do grupo mais proximamente relacionado a estes gêneros como grupo externo diminuiria as possibilidades de homoplasias entre grupos distantes, ou seja, bases compartilhadas entre gêneros não relacionados filogeneticamente, causando “noise” e resultando em uma árvore com pouco suporte de bootstrap.

Mas, como não foi possível acessar o grupo mais proximamente relacionado com *Angelphytum* e *Dimerostemma*, resolvemos utilizar os marcadores ITS1, ITS2 e ETS para 19 acessos de 18 espécies de *Angelphytum* e *Dimerostemma*, como também para 39 espécies representantes de 32 gêneros de Ecliptinae e de 3 gêneros como grupo externo. Estas regiões não codificantes do DNA nuclear têm sido valiosas na reconstrução da filogenia de plantas, especialmente em nível específico. Na árvore de consenso observa-se que a maioria dos dos nós internos encontra-se bem sustentado, com bons valores de

bootstrap, o que no entanto, não acontece para os nós basais, denotando uma rápida radiação genérica. Acreditamos que a radiação recente dos gêneros de Ecliptinae seja a causa de poucos caracteres moleculares distintivos em ITS e ETS.

As diferenças em expressão de caráter entre os gêneros de Ecliptinae são usualmente tênues, por isso os limites taxonômicos da maioria deles têm se revelado bastante incertos. As relações intergenéricas derivadas da análise filogenética, utilizando seqüências do DNA nuclear, ajudam a esclarecer, onde dados e amostragens permitem, os limites taxonômicos na direção da monofilia dos gêneros de Ecliptinae.
A diferença morfológica entre *Angelphytum* and *Dimerostemma* reside na sexualidade das flores periféricas, estéril em *Dimerostemma*, fértil em *Angelphytum*. Exceto por este caráter, *Angelphytum* é essencialmente idêntico a *Dimerostemma* em todas as demais características. Nosso resultado mostra que o gênero *Dimerostemma* é parafilético com a exclusão de *Angelphytum* e que as espécies destes dois gêneros compreendem um grupo monofilético fortemente sustentado. Este resultado e a ausência de evidências morfológicas para a divisão entre estes gêneros indicou a combinação de *Angelphytum* sob *Dimerostemma*.

***Sobre os marcadores moleculares*:** A matriz de dados resultante das análises moleculares utilizando nove regiões de cpDNA soma um total de 8052 caracteres (pares de bases). Entre estes, 551 apresentaram-se variáveis, sendo que 299 (3,7% do total) foram filogeneticamente informativos. As regiões do ITS1, ITS2 e ETS do DNA nuclear forneceram uma matriz de dados com1397 caracteres. Deste total, 654 mostraram-se variáveis com 453 (32,4% do total) apresentando-se filogeneticamente informativos.

Resumindo, apenas 3,7% do total de caracteres provenientes das regiões amostradas do cpDNA apresentaram-se filogeneticamente informativos contra 32,4%

daqueles oriundos das regiões do DNA nuclear. Desta forma, conclui-se que entre os marcadores utilizados, os de DNA nuclear mostraram-se muito mais eficientes em providenciar caracteres variáveis e filogeneticamente informativos.

Entretanto, à esta vantagem dos marcadores de DNA nuclear aliaram-se duas desvantagens: 1) foi mais difícil amplificar seqüências de boa qualidade provenientes do DNA nuclear do que do cpDNA. Implicação disto é que certos pedaços das seqüências do DNA nuclear, principalmente aqueles localizados nas extremidades, freqüentemente apresentaram bases ambíguas, e 2) por apresentarem grande variação de caracteres, as seqüências do DNA nuclear foram mais difíceis de alinhar. Além disso, deleções e inserções de um grande número de bases foram freqüentes nestas regiões, dificultando em muito o alinhamento.

Ao contrário, de uma maneira geral, foi mais fácil amplificar seqüências de boa qualidade do cpDNA, evitando assim as bases ambíguas. Como geralmente foram menos variáveis, com deleções e inserções menores salvo algumas excessões, as seqüências das regiões amostradas do cpDNA também foram mais simples de alinhar. Conseqüentemente, as seqüências do cpDNA conduziram à obtenção de uma filogenia mais fidedigna.

Um outro aspecto a ser apontado refere-se à análise de parcimônia máxima. Os dados combinados do cpDNA resultaram em 3600 árvores igualmente parcimoniosas, cada uma com 1105 passos (transformações de caráter) e índice de consistência (CI) de 0,63 (excluindo autapomorfias). Já os dados combinados de DNA nuclear resultaram em 9 árvores igualmente parcimoniosas, cada uma com 2088 passos e CI = 0,42 (excluindo autapomorfias).

Fica difícil a comparação dos índices, pois os dados combinados de cpDNA foram obtidos para 62 acessos, enquanto os do DNA nuclear foram conseguidos para somente 36. O índice de consistência mede a homoplasia (semelhança de estruturas não

homólogas) em um cladograma. Quanto mais próximo de 1 (valor máximo), menor a quantidade de caracteres homoplásicos. A árvore proveniente do cpDNA apresenta um menor número de caracteres homoplásicos, indicando portanto uma topologia mais consistente.

Contudo, estes marcadores também apresentam restrições. Como é necessária a utilização de vários marcadores do cpDNA para a obtenção de uma quantidade razoável de caracteres variáveis, surge um ponto de estrangulamento. O limite reside justamente no custo das várias seqüências e na necessidade de uma maior quantidade de DNA total, nem sempre possível de ser obtido para alguns dos táxons envolvidos.

Até onde é confiável e permanente os resultados de uma análise filogenética? A experiência com uma grande matriz de dados mostra que adições de novas porções de dados somente solidifica o sinal filogenético e suporte dos ramos (Panero & Funk, 2002). Fica claro nestes estudos que, depois de um certo ponto, único para cada série de dados e determinado pelo número de caracteres e táxons amostrados, o sinal filogenético estabiliza. Desta forma, a adição de novas porções de dados no futuro irão somente solidificar o suporte dos ramos. Para a obtenção de uma filogenia fidedigna, destacamos a necessidade de inserir nas análises uma boa amostragem do grupo em estudo.

Nos casos onde o custo é o principal fator limitante, os marcadores mais variáveis, como o ITS e ETS são os mais indicados. Convém, no entanto, ter em mente que o alinhamento deverá ser criterioso. Pode-se utilizar de estratégias que ajudem no alinhamento, tais como a descrita por Baldwin *et al.* (2002). Estes autores descreveram um processo manual interativo de alinhamento de seqüências para as regiões de ITS1 e ITS2. Grupos de uma matriz inicial de seqüências que apresentassem um bom suporte (≥85%), tendo como base valores de “fast heuristic” bootstrap, foram usados como guias para um refinamento subseqüente do alinhamento. O alinhamento é otimizado dentro de cada grupo antes do reconciliamento entre os grupos.

No caso de não haver nenhuma análise filogenética prévia dos táxons envolvidos, a estratégia descrita por Baldwin *et al.* (2002) é adequada. Em nosso estudo, além de utilizarmos a estratégia descrita acima, também usamos uma outra. Aqueles grupos que apareceram com um bom suporte de boostrap nas análises do cpDNA foram, por sua vez, empregados como guias no processo manual interativo de alinhamento de seqüências de ITS1, ITS2 e ETS.

Tratamento taxonômico: Por último, o terceiro capítulo refere-se ao tratamento taxonômico para as espécies brasileiras. As relações entre as espécies de *Dimerostemma* ocorrentes no Brasil foram avaliadas morfologicamente, principalmente por meio do exame cuidadoso das características referentes à cipsela. O estudo taxonômico serve como um guia para o entendimento dos resultados provenientes dos estudos moleculares. Estes, por sua vez, alertam para alguma característica não apreendida no exame morfológico ou confirmam as já observadas.

Assim, a distinção de *Dimerostemma annuum* como o único membro do grupo que se apresenta como uma herbácea anual delgada e que possui páleas levemente conduplicadas é sustentada pelas seqüências do DNA nuclear, aparecendo como táxon basal nas análises moleculares. A similaridade das folhas e cipselas entre *D. apense*, *D. herzogii* e *D. bahiense* confirma uma relação filogenética entre estas espécies, uma vez que estas encontram-se agrupadas no mesmo clado. Por apresentarem cipselas muito parecidas, alguns espécimes de *D. arnottii* com folhas estreitas e curtas são bastante semelhantes a *D. reitzii*. A similaridade entre estas espécies também é apoiada pelas análises moleculares, indicando um relacionamento filogenético próximo.

As espécies *D. lippioides*, *D. brasilianum* e *D. vestitum* ocorrem freqüentemente em Goiás e Minas Gerais, onde crescem lado a lado e florescem ao mesmo tempo. Estas espécies compartilham entre si folhas largamente ovadas a orbiculares, com uma grande

porção de seus espécimes facilmente separados por características da cipsela. Entretanto, estas espécies formam um complexo com indivíduos intermediários entre si. Os dados moleculares confirmam as afinidades entre estas espécies e esta variação em características morfológicas pode ser resultado de hibridação.

A ausência de alas associada com a forma quadrangular da cipsela parece não representar uma relação filogenética entre *D. vestitum*, *D. bishoppii*, e *D. specie nova*, pois estas espécies se encontram espalhadas no cladograma, indicando que esta tão óbvia característica morfológica pode não corresponder a uma afinidade filogenética.

Finalizamos afirmando que as análises moleculares podem sustentar uma decisão taxonômica que, sem este apoio, poderia ser interpretada como subjetividade do taxonomista. Desta forma, os ajustes taxonômicos realizados em prol da monofilia dos táxons, principalmente se aliados à morfologia, raramente enfrentam controvérsia. O exame morfológico das espécies é o caminho que mais aproxima o pesquisador do seu objeto de estudo. Ao considerar as potencialidades da filogenia molecular, não esquecendo de suas limitações referentes ao custo e alinhamento das seqüências, e ao considera que é a morfologia que dá subsídios para a compreensão daquilo que observamos na naturea, nós teremos então a ampliação do nosso conhecimento botânico.